Mating Behaviours of the Field Cricket (*Gryllus integer*) at Different Levels of Male Density

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ABSTRACT

The reproductive behaviour of the field cricket, Gryllus integer, was systematically observed in indoor arenas to determine the extent of female choice and male-male competition at different sex ratios representing two male densities (12:6 and 6:6). The costs and benefits to males and females in those two densities were analyzed according to the theory of the evolution of leks. Observations were conducted during the dark hours when most calling occurred since hourly rates of courtship song and mating did not fluctuate significantly over a 24 h period. Female mating rates were not significantly different between densities, therefore males at high densities were not advantaged because of increased female tendencies to mate when social stimulation was increased. Mean rates of acoustical signalling (calling and courting) did not differ significantly between densities. Mean rates of fighting by males at the high density were significantly greater than those of males at the low density.

Mating benefits associated with calling, courting and fighting were measured. Mating rates did not vary with rates of calling at either density. Calling was not a prerequisite to mating. Courtship song preceded all matings. There was a significant power fit between male mating and courting rates, and male mating and fighting rates at the low, but not at the high, density. Density differences in the benefits associated with increased courting and fighting may relate, in part, to greater economic defensibility and monopoly of females due to reduced male competition at the low density.

Dominant males may be preferentially chosen by females or better able to monopolize mating opportunities than subordinate males. Three criteria were used to determine whether dominant males were preferentially chosen by females. The number of matings by males who won fights (within 30 min of mating) was significantly greater than the number of matings by males who were defeated in such fights. Mating rates did not vary significantly with rates of winning at either density. There was a significant power fit between male mating rates and the percentage of fights a male won (irrespective of his fighting frequency) at the low density.

The mean duration a male guarded the female after mating did not vary significantly between densities. There was a significant linear relationship between the duration a spermatophore was retained and the duration a male guarded the female after mating. Courtship song apparently stimulated spermatophore removal. Male guarding involved inter-male aggression and reduced courtship attempts by other males.

Males at the high density received no apparent reproductive benefits associated with increased social stimulation. Conclusive evidence for preferential choice of males by females, using the criteria examined here, is lacking. Males at the lower density had fewer competitors and could monopolize females more effectively.

To Jim

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INTRODUCTION

Darwin (1871) identified two interrelated selective forces affecting reproduction. These are referred to as intrasexual selection, (usually expressed as male-male competition), and intersexual selection, or preferential choice of mating partners by one sex (primarily an attribute of females). One of the key parameters affecting these forces is the relative amount of investment by parents in offspring (Trivers 1972). In species where males contribute little but spermatozoa to offspring, their reproductive success is enhanced by fertilizing as many eggs as possible. By contrast, females invest heavily in offspring by virtue of their production of eggs and in some cases subsequent care of offspring. Females should therefore mate with high quality males hence enhance the quality of their offspring (Trivers 1972).

Male-male competition can occur before, during or after copulation. Precopulatory competition for females may take the form of territoriality or dominance hierarchies, whereby an individual male restricts the access of females to other males. Aggressive behaviour in the context of territoriality or dominance is usually expressed as some form of visual, acoustical or olfactory signalling, and by fighting behaviour. Competition during and after mating may take the form of remaining in copula for extended periods (Wells 1977) or guarding the females after insemination (Parker 1970a). In both cases other males are prevented from copulating with the recently

mated female. Male-male competition has been studied in a variety of species (e.g. Howard 1978, LeBoeuf 1974). By contrast, few studies have concentrated on female mating preferences (Emlen and Oring 1977). Female mating preferences may involve mating with sexually competent males or copulating preferentially with males of a specific genetic constitution (Trivers 1972).

Various parameters can influence the intensity and direction of sexual selection. In acoustical insects and other species where males form mating aggregations the operational sex ratio (OSR), defined as the average ratio of fertilizable females to sexually active males at a period in time, is of importance (Emlen and Oring 1977). Reproductive competition will be affected by male density. At low densities males can monopolize resources (e.g. females) if they are economically defensible; however, at increasing densities, territorial defense of resources is a decreasingly viable option for males (Brown 1964). Increases in the intensity of mate attraction signals, and the distance signals are transmitted when male density is great, rarely lead to increases in the number of females attracted to aggregations on a per male basis (Bradbury 1981). However, males may experience reproductive gains by aggregating if females prefer clustered males over dispersed males (Bradbury 1981). Using isolated and clustered loudspeakers broadcasting male cricket (Gryllus integer) calling song, Cade (1981b) found experimental evidence suggesting that increases in the number of females attracted per male do not result when aggregation size is increased. However, females may be stimulated to mate, to a

greater extent, when male numbers are greater (Darling 1938, Lott et al. 1967).

Field crickets (Orthoptera, Gryllidae) are ideal specimens for examining the processes of sexual selection. They are nocturnal and inhabit most large land masses. Cricket signalling behaviour primarily involves acoustical communication by males. In many cricket species, males form loose aggregations within which they call. The calls result in the attraction of females to the aggregation and the repulsion of other calling males from an individual's immediate calling site. Signalling sites are acquired by inter-male fighting within the aggregation. The production and elements of the call (e.g. intensity, duration, frequency) may provide important criteria by which females choose mates (Crankshaw 1979).

This study used indoor arenas to examine the effects of two male densities on male-male competition and female choice in the Texas field cricket Gryllus integer.* Literature on sexual selection theory, the sequence of mating in field crickets and the effects of population density on mating behaviour in a variety of species are reviewed. Experimental results and observations on the reproductive behaviour of males at two densities (N=six and twelve) and females (N=six) in indoor arenas are presented and discussed.

*This species is currently under taxonomic revision and will be called Gryllus texansis (Cade and Otte in press).

LITERATURE REVIEW

Sexual Selection Theory

The theory of sexual selection consists of two components, intrasexual selection (competition within one sex for members of the opposite sex) and intersexual selection (preferential choice by members of one sex for individuals of the opposite sex) (Darwin 1871). These two components are often inseparable, but both are thought to have a role in the evolution of adaptations associated with reproduction.

Selective forces act differently on the sexes because of differences in the parental contributions to the offspring (Bateman 1948, Trivers 1972). Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chances of survival while reducing the parental investment to other offspring." In general, females invest more heavily in offspring. The reproductive success of the female is limited by the number of eggs that she has, nutritional investments in the relatively large eggs, and, in some species, investment in the offspring. In most cases, the reproductive success of the male is limited by the number of females he can inseminate with his relatively small and inexpensive gametes.

The lifetime energies of an individual may be considered to consist of somatic and reproductive effort (Hamilton 1967, Williams 1966). Low (1978) separated reproductive effort into parental and mating effort. Parental effort is the sum of parental investment over the lifetime of an organism. Mating effort consists of intrasexual competition, attracting or locating

mates and/or acquiring resources (Alexander and Borgia 1979). In species characterized by low male parental investment and consequently high mating effort, some form of intrasexual competition will predominate. It is often proposed that males providing varying degrees of mating effort will have varying chances of mating success, and that the males will evolve extravagant characters and/or provide vigorous courtship, aphrodisiacs, nuptial gifts or other material benefits to charm the female (Wade and Arnold 1980). Females become discriminating of male displays in order to increase the certainty of male quality. Williams (1966) described the tactics of both sexes as an evolutionary battle of the sexes involving highly skilled salesmanship among males and equally well-developed sales resistance and discrimination among females.

Male-male competition serves several functions which enhance the probability of increased male mating success. Males may physically compete with each other in order to achieve dominance status, for example, in the European Ruff, Philomachus pugnax, (Hogan-Warburg 1966) and Elephant seals, Mirounga anguistirostris, (Leboeuf 1974). Males may compete using signals important in mate attraction, for example, in the scorpianfly Panorpa (Thornhill 1973) and the black-tipped hanging fly Bittacus (Thornhill 1979) males emit pheromones to attract females to a nuptial gift. In the field cricket, Gryllus integer*, males may call to attract females (Cade 1979a). Pheromonal or acoustical signals produced by some males may be stronger and outcompete or interfere with those of other males (Alexander 1975, Otte 1977).

Males may also compete in terms of the resources they offer females. Gifts of prey are offered by males to female scorpianflies and hanging flies (Thornhill 1976a,b). Some Orthopteran males provide glandular secretions (Alexander and Otte 1967, Bell 1979a) or sperm packages in the form of spermatophores (Alexander 1961) or spermatophylaxes (large proteinaceous sperm packages) (Gwynne 1981). Males offering greater gifts are often preferred by females. Males may compete to monopolize territories essential to the reproductive success of the females. For example, in the bullfrog, Rana catesbiena, males who defend territories in the water, which are conducive to embryo development and success, are often preferred by females (Howard 1978). Males may also have differential abilities to find mates (Parker 1970b). Alcock (1979) described patroller or hoverer strategies which involve aggression and no aggression respectively in Centris pallida, a bee.

Males may also compete intrasexually after mating by having sperm of different mobilities or different displacement properties. Parker (1970b) defined sperm displacement as "the displacement of previously stored sperm and its replacement with sperm from the last male to mate." Sperm may have different fertilization properties and/or varying abilities to induce non-receptivity in females.

Criteria which females may employ in their choice of males are more difficult to identify. Female choice may be based on signals (visual, acoustic, tactile or olfactory) which identify the male as being of the correct species. A male's relative genetic quality may also be used in female choice (Borgia 1979).

Male genetic quality may be demonstrated by a male's participation and success in aggressive encounters. Such encounters permit the female to assess quickly and inexpensively relative male qualities. Alexander (1975) suggested that females choose among males according to their fighting ability since resultant sons may also fight well and may be preferred by females in mate choice. This is possible if male fighting ability is correlated with greater than average genetic quality among offspring of both sexes and females choosing aggressive males experience a net gain. However, strong sexual selection should drive a preferred trait to fixation. Such traits hypothetically will have low heritability (West-Eberhard 1979). Borgia (1979) suggested that when selection pressures are shifting, genetic variability is maintained. Cade (1981a) found that the duration of male calling, presumably under strong sexual selection, has a high heritability. This may be a result of varying selective pressures from the parasitic fly, Euphasiopterix ochracea, which oviposits on calling males and associated females.

Dominant males may have greater resource holding power (Parker 1974) or perform qualitatively or quantitatively more attraction and courtship behaviours. Females have been shown to choose dominant males over subordinate males in the house cricket, Acheta domesticus (Crankshaw 1979). In the field cricket, Teleogryllus oceanicus, dominant males sing more than losers (Burk 1980). Dominance status may be related to male size, for example, in the soldier beetles, Chaulignathus pennsylvanicus, (McCauley and Wade 1978), Drosophila melanogaster (Dow and von Shlicher 1975) and the cockroach, Gromphadorina brunneri, (Zeigler 1972).

Fisher (1930) argued that females could increase their offsprings' reproductive success if they chose males with a preferred survival-related feature. He suggested such a feature would become exaggerated through the process of run-away selection until natural selection offset the benefits of such a feature. Specifically, females selecting males with a given trait would get an initial benefit because of a survival advantage. Their male offspring would have this survival-related trait and their daughters would prefer males with such a trait. This would lead to males possessing this trait gaining an advantage in the population. In this manner, the trait would continue to be exaggerated until natural selection intervened and the character reduced survival. Zahavi (1975) suggested that females should select males on the basis of traits that are phenotypic indicators of the male's ability to survive, despite his possession of a handicap which reduces his chances of survival. Several models have been proposed since Zahavi suggested the "handicap principle" and indicate this principle will only be valid under restrictive circumstances (Bell 1978, Davis and O'Donald 1976), and involves the continual monitoring and evaluation of risks to the male by the female in different environmental conditions (Thornhill 1976b).

Females may control their site of capture by males (Borgia 1979) or the timing and direction of their approach (Thornhill 1979) in cases where males capture females and prevent their future mating.

Females may also choose males on the basis of material benefits, in the form of resources, which they control or possess. In the hanging-fly, Bittacus, females prefer males who provide

large nuptial gifts and will sustain copulations with them for longer periods than they would if males provided small gifts (Thornhill 1976b, 1979). In the dragonfly, for example, Plathemis lydia, females choose males according to oviposition sites within their territories (Jacobs 1955). If material benefits limit female reproduction an equilibrium will be established between the amount of material benefits a male can offer and the amount a female can demand and accept (Borgia 1979).

Females may choose rare males. Such choice has been suggested in Drosophila (Petit and Ehrman 1969) and the guppy, Poecilia reticulata, (Farr 1975). Females may select males of rare phenotypes in which differences in traits are based on differences due to single mutations or chromosomal inversions. Examples of females selecting males possessing such differences have been given as evidence for genetic choice in which females are programmed to select males based on differences of a single gene and thus complement alleles in the females gametes (Ehrman and Parsons 1976).

Females may also choose males according to their mating experience. For example, in the pigeon, Columba livia, experiments of mate choice showed females choose experienced males over inexperienced males (Burley and Moran 1979).

Acoustical Insects

Gryllus integer is a member of the order Orthoptera, family Gryllidae, crickets. Field crickets are found in the soil surface or shallow burrows. They are omnivorous and occur in most territorial habitats between 44° north and south latitude (Alexander 1968).

Many crickets exhibit dispersing abilities. There are long-winged individuals (macopterous) and short-winged (micropterous) individuals. Changes in temperature, photoperiod, density, and diet alter the proportion of long-winged individuals in lab populations (see references in Harrison 1977). Environmental factors during sensitive periods in an individual's life apparently affect wing development (Harrison 1977) although a genetic polymorphism is also likely important (Alexander 1967).

With few exceptions, male crickets provide no parental investment beyond their sperm and females end their parental investment at oviposition (West and Alexander 1969). Although males show little parental investment, their mating effort is increased. Mating aggregations of males are formed during the breeding season, and intramale aggression is intense during this period. Intramale competition is expressed most apparently as acoustic signalling, however males may also acquire females by silent searching and waiting for females in the area of acoustically signalling males (Cade 1979a). Alexander (1961) used a five-level scale to describe the intensity of aggressive encounters in male Gryllus which is as follows:

Level One - Contacts between males are terminated without apparent aggression or apparent retreat.

Level Two - Contacts are terminated by retreat without apparent aggression.

Level Three - Contacts are terminated by retreat after mild to moderate one-sided aggression or mild reciprocal aggression.

Level Four - Contacts are terminated after moderate to intense reciprocal aggression.

Level Five - Contacts are terminated only after sustained combat.

The Mating Sequence

The functional elements of a mating sequence in Gryllus and other field crickets involve mate attraction, pair formation, stridulatory and antennating behaviours, copulation and post-copulatory behaviours primarily involving guarding the female and preventing access by other males (Alexander and Otte 1967, Loher and Rence 1978). Each of these elements will be discussed in detail.

Mate Attraction and Pair Formation

The production of intense, persistant, rhythmic sounds are characteristic of many species of Orthoptera (Alexander 1961, Walker 1957). Calling songs are produced by the adult male by scraping a file on the forewings (on the upper tegmina) against the median edge of the lower tegmina (Alexander 1957). The basic unit of the calling song is the pulse, each chirp is made up of a sequence of pulses (Zaretsky 1972). The intensity of the song varies within and between individuals (Cade 1979a). The sound intensity depends on the resonance properties of the tegmina or parts of it (Nocke 1971). The sounds are perceived by tympannal organs located on the forelegs (Popov and Shuvalov 1977). Walker (1957), Alexander (1957) and Alexander and Thomas (1959) have shown that cricket songs vary little in structure among individuals of a species. Differences between species are the result of genetic differences (Alexander 1957, Bigelow 1960). Call production is regulated by the presence of a spermatophore in the spermatophore pouch (Huber 1955) daily cycles of light and dark, physiological changes associated with failure to copulate and by another male's calling. Male crickets generally spend one to nine hours

of every twenty-four in acoustic behaviours (Loher 1972), Walker 1979), during discrete periods determined by light and/or temperature and humidity (Alexander 1957). Cade (1981a) has shown that the amount of calling per night has a large genetic component in G. integer.

Males generally sing from the same place for extended periods of time (Loher 1979) and by doing so cause females to locomote, (Haskell 1953) be attracted and subsequently copulate (Alexander 1961, Popov and Shuvaluv 1977, Ulagaraj and Walker 1973 , Walker 1957). In addition, male calling also serves in spacing males because calling indicates aggression (Alexander 1961). Calling may also indicate a suitable habitat for females (Ulagaraj and Walker 1973) and one which may contain females (Cade 1979a, 1981b). Conspecific males, some of whom may be stimulated to call or adopt silent, searching, satellite behaviours (Cade 1979a) may also be attracted. Predators, such as cats (Walker 1964) or the Little Blue Heron, Florida caerulea, (Bell 1979b) as well as parasitoids which deposit eggs or larvae such as the parasitic fly, Euphasiopterix ochracea, may orient to G. interger males and females (Cade 1975) and Scapterius vivinus and S. acletus (Mangold 1978).

Weih (1951) and Busnel et al. (1956 in Walker 1957) found males of seven species of grasshoppers (Orthoptera:Acrididae) and five species of pygmy grasshoppers Ephippigeridae respectively, responded to songs of other males by singing in regular alternation. This increases the regularity of song production through time and results in an increase in the number of females attracted (Alexander 1967). Calling songs are thought to be a species isolating mechanism (Marler and Hamilton 1967). Species specific phonotactic

responses have been demonstrated in many species (see Popov and Shuvaluv 1977 and references therein). The importance of calling song in species isolation is demonstrated in species which share a common habitat and breed synchronously. Such species have distinct calling songs (Alexander 1967, Walker 1957). Species which are either temporally or geographically separated may have similar songs. For example, the spring field cricket, G. veletis, and the fall field cricket, G. pennsylvanicus, in eastern North America, have similar calling songs (Alexander and Bigelow 1960). Hill et al. (1972) provided evidence that female field crickets, T. commodus and T. oceanicus, discriminated between sympatric and allopatric male calling songs if they were produced simultaneously. Paul (1976) found that female ground crickets (Gryllidae:Nemobinae) would respond preferentially to conspecific male calling song when given a choice but in the absence of choice responded to heterospecific male calling song. He concluded that the female response to the calling song is important in prezygotic reproductive isolation but alone is not sufficient to prevent inter-specific courtship and mating in mixed species. Popov and Shuvalov (1977) predicted that the recognition and choice of male calling songs by females works on a probability principle; females choose songs that have a high probability of being conspecific. Species specificity or calling song can reduce time and energy used in finding, courting and mating.

Several experiments have provided information on what elements of the calling song and modes of perception are of importance to a female's correct identification of species and sex. Busnel and Busnel (1954 in Walker 1957) showed that the responsiveness

of female tree crickets, Oecanthus pellucens, depends on their phase in the reproductive cycle. Young female house crickets A. domesticus, demonstrate negative phonotaxis to all sounds perceived by their tympannal organs for several days after their final molt (Shuvalov and Popov 1971), however, they eventually develop positive phonotaxis as they age (Popov and Shuvalov 1977). Cade (1979b) showed that male-deprived female field crickets, G. integer and G. veletis, are more readily attracted to conspecific mating songs than females exposed continuously to males. In addition, Cade (1979b) demonstrated an increased level of phonotaxis within three days of female separation from the male.

Walker (1957) found that the pulse rate of the male calling song in tree crickets, Oecanthus spp, varied with temperature, as does the female response. Zaretsky (1972) artifically altered the chirp intervals of male crickets, Scapsipedus marginatus, then eliminated the sound for fixed periods after each chrip. His results indicated that the interval between chirps was not crucial to female attraction unless they were in excess of 25 seconds apart. It appeared that females lost the ability to locate the sound source because of inadequate directional information during the silent intervals to compensate for the female's random movements. Female T. oceanicus follow a slightly zigzag course as they move to a species specific sound source (Hill et al. 1972). The carrier frequency of the calling song is important for female response but not a basic cue for recognition since the tympannal organs respond with maximum sensitivity near the fundamental frequency of the conspecific calling song which may overlap with sympatric species (Zaretsky 1972). Busnel and Loher (1954 in Walker 1957) found that artificial signals of higher intensity

than the normal song induced responses in the grasshoppers Chorthippus jucundus, C. brunneus, and C. bigattalus, similar to responses for natural intensities. The tympannal organs are of vital importance to a female in locating a sound source as is evidenced in the circular movements of females whose tympannal organs have been destroyed (Zaretsky 1972).

Calling appears to be an effective means of communication in that it attracts females and spaces males. However, many species have lost their calling song (Otte 1977, Walker 1974). For example, the Florida field cricket, G. ovisopis, does not have a calling song although a sympatric species, G. fultoni, has retained it. It has been suggested that the selective forces which have caused G. ovisopis to lose its song relate to the emergence of parasitic flies during similar times of the year as adult crickets. Those individuals who have survived in spite of the parasitic fly, likely those who employ olfactory senses to a greater extent, have differentially reproduced. Gryllus ovisopis males apparently relinquish some of the costs of calling by adopting silent, sedentary habits.

Courtship

Females who are sexually responsive can orient to male courtship song as well as male calling song (Alexander 1962). Courtship song is usually initiated by the male. Contact preceeds mutual attennation and the female becomes sedentary (Alexander 1961). The courtship sequence consists of a characteristic courtship song and characteristic body movements (Alexander and Thomas 1959, Alexander 1967). The courtship song is of lower intensity than the calling song, and is produced by the scraping of wings

(however, with less pressure than in the calling song) (Alexander 1961). The pair become positioned with the male in front of the female. When a sexually responsive female walks up the back of a courting male her orientation is aided by the vibration of the male's cerci along the sides of her abdomen (Alexander 1961). Successful courtship culminates in copulation.

Courtship may give the female indications of male quality (Kirkendall unpublished ms.) and indications of future male parental investment (Thornhill 1979). To the male, courtship behaviours may act in reducing female coyness and displaying male quality. Courtship in some Orthopteran species involves emission of the song and/or attracting glands. In general, when female attracting glands are present, for example in tree crickets, Oecanthinae, the courtship song is intermittent and not distinctive; but when such glands are absent, for example in Acheta, courtship sounds are rhythmic, continuous and distinctive (Alexander and Thomas 1959). Courtship is similar throughout species of Acheta and Gryllus (Alexander and Thomas 1959, Otte and Cade 1976). Pheromonal cues may also be used in attracting females and reduce the need of the courtship song (Otte and Cade 1976). Antennae are equipped with chemical and tactile receptors and may be used to detect such cues (Loher and Rence 1978). Courtship in some species may be a species specific identification signal (Crankshaw 1979).

Copulation

In crickets, the female mounts the male in copulation (Alexander and Thomas 1959, Alexander and Otte 1967). The male flattens his body against the substrate and backs towards the female until contact is made. The female may mount the male or the male will

ease backward under the female until she climbs on him (Alexander 1961). The female lowers the tip of her abdomen, and the male seizes the bursa copulatorix at the base of the ovipositor with his epiphallic hook. The male extrudes the spermatophore and threads it into the subgenital plate (Alexander 1961).

In the house cricket, A. domesticus, mature sperm begin to migrate from the testes into the seminal vesicles at three to four days after the adult molt (Murtaugh 1980). Male house crickets are sexually mature about six days after adult eclosion and males are capable of calling at this time (Murtaugh 1980, Wyatt in prep.). Female T. commodus can mate within 24 hours of adult eclosion if they are placed in a cage with a mature male (Loher and Edson 1972) however, females cannot be attracted to males in nature before a day or two post eclosion (Loher 1979).

The duration of copulation in a given species will be influenced by selective pressures on the male to reduce sperm competition and insure insemination before oviposition (Alexander and Otte 1967) to achieve sperm precedence (Parker and Smith 1975) and to increase the number of females he can inseminate (Alexander and Otte 1967). The female, on the other hand, may be under conflicting pressures to reduce or increase the number of matings to ensure high quality paternal genes, or increase genetic diversity in her offspring. She should be selected to reduce time in copula if it has negative effects on her survival because of increased risks to predation or harm. Daly (1978) reviewed the costs of mating to the female in a wide variety of animals. Increased time in copula is expected if it increases female survival. Copulatory gifts, which represent direct or indirect male parental

investment, may increase the survival probability of offspring, or female longevity and hence increase overall productivity (Thornhill 1976a).

Copulations in field crickets generally last from a few seconds to several minutes, with most species taking less than one minute (Alexander 1967). A relatively brief copulation may be less expensive to both sexes than resistance in terms of time, energy, risk of resource usurpation, physical injury and/or exposure to predation or parasitism (Alcock 1975). The physiological and morphological limitations of passing sperm by an osmotic process (Khalifa 1950) or pressure system (Fulton 1931) may influence the duration of copulation in some insects.

The gryllid spermatophore consists of a thick three-layered mass around a membranous sperm sac and a long tube continuous with the outer layers (Khalifa 1950). Spermatophores are rich in proteins (Khalifa 1950), in addition they represent a nutritious substance and their production has been considered part of the male's mating effort since it is a necessary prerequisite to mating (Alexander and Borgia 1979). However, female consumption of the spermatophore, combined with subsequent loss of female sexual receptivity, suggest that it is male parental investment (Morris 1979). Sakuluk and Cade (1980) suggested that spermatophore feeding is a form of mating effort. Since highly mobile females often mate with different males, the probability that the male contributed nutrition into the eggs he fertilizes by way of the spermatophore is reduced. They further suggested that males selected to invest parentally should produce large spermatophores rather than the small and simple ones characteristic of

A. domesticus and G. integer. In some other crickets and katydids, the spermatophore may have evolved in the context of parental investment. For example in the grasshopper, Ephippiger bittrensis, the spermatophylax makes up to 25 percent of the male body weight (Busnel et al. 1956 in Walker 1957).

The frequency and interval between matings depends, in part, on the number of spermatophores a male can produce (Alexander and Otte 1967, Loher and Rence 1978). In T. commodus, males produce one spermatophore per 24 hours in isolation. Spermatophore production is under circadian influence (Loher and Rence 1978).

Guarding Behaviours

In many crickets, a male will prevent the female from moving by antennating the female or aggressively rocking until he forms a spermatophore (Loher and Rence 1978). Males may also allow the female to consume glandular secretions he produces or his own body (Bell 1979a Walker 1979). For example, tree crickets of the genus Oecanthus and Neoxabea produce glandular secretions in metanotal glands located under their wings upon which females feed during copulation (Bell 1979, Walker 1979). None of the Gryllinae are known to possess a dorsal gland or other structure involved in inducing females to copulate (Alexander and Thomas 1959). In Oecanthus spp. Bell (1979a) suggested that the metanotal gland may be used to allow full insemination of the female, attract females, prevent heterospecific matings and serve as a source of nutrition. He found that the number of eggs laid by O. nigricornis increased with the number of spermatophores and amount of glandular product consumed by the female. In addition, females

consume the fleshy wings beneath the tegmina of the male tettigonid, Cyphodermis buckelli, (Morris 1979). Post copulatory behaviours, as described above, are thought to function in keeping the female near the burrow of the male and allow him to copulate with the female repeatedly (Alexander and Thomas 1959). These behaviours also prevent the female from removing and eating the spermatophore before it is emptied of sperm (Alexander 1967). However, Sakuluk and Cade (1980) found that female house crickets A. domesticus, separated from males after mating had spermatophore retention time similar to the females kept with males.

Oviposition

Gryllid females will copulate repeatedly without ovipositing for a day or two, but will lose sexual receptivity if not allowed to oviposit (Alexander and Thomas 1959). Oecanthinae and Neoxabea crickets prepare for oviposition by chewing a small pit in the bark of a plant then deposit eggs and a mucilaginous substance over the hole (Fulton 1918). Female Anurogryllus lack well-developed ovipositors and lay eggs in underground burrows (Walker 1979). Gryllus females require moist soil for oviposition (Alexander and Thomas 1959). Oviposition in Gryllus takes place over a considerable period of hours and females move little during this period; however, like T. commodus, they will cease ovipositing and mount courting males (Loher and Edson 1973).

Total egg production and oviposition rates are influenced by mating. Mating increased total egg production in T. commodus, and Plebiogryllus guttiventris (Bentur et al. 1977 and references therein). Furthermore, mating is a prerequisite to oviposition in many insects (Engelmann 1970). Mechanisms involved in these

changes may be due, at least in part, to the response of the spermatheca to mating, notable triggering of the pars intercerabralis or corpora allata to release gonadotrophic hormones which stimulate oocyte production and the ovipositing response (Bentur et al. 1977, Loher and Edson 1972). Also secretions transferred through the spermatophore (Bentur et al. 1977, Loher and Edson 1973) or accessory gland (Pickford et al. 1969) and prostaglandins (Destaphano et al. 1974, 1976, Loher 1979) lead to increases in egg production and oviposition rates in A. domesticus and T. commodus.

Multiple Mating

Multiple mating is a common phenomenon in the insects, although the adaptive significance is often unclear (Wigglesworth 1965). Sperm retain fertilization capacity through much of adult female life (Davey and Webster 1967). In most insects, eggs are fertilized at oviposition with sperm stored by the female from previous matings (Parker 1970b). Experiments with genetic markers have shown that the last male to mate prior to oviposition usually has precedence of sperm, although sperm mixing may occur in some cases (Parker 1970a). Sperm precedence may occur by mechanisms associated with the male's reproductive organs (see Waage 1979) or differences in the quality or quantity of transferred sperm which enhance their fertilization abilities (Childress and Hartl 1972, Parker and Smith 1975, Walker 1980).

There is a selective advantage to the male in attaining mechanisms that increase the chances of paternity by sperm displacement and/or precedence and counterselection will favour mechanisms which reduce the effectiveness of subsequent matings (Kirkendall unpublished ms.) and to induce or overcome female

nonreceptivity to subsequent matings (Cobbs 1977). Males may increase the probability of their sperm being utilized by pre- or post-copulatory guarding behaviour, mating plugs, chemical or physical properties of the ejaculate which decrease female receptivity to remating, sperm displacement (Parker 1970a) or sperm precedence (Gromko and Pyle 1978).

Multiple matings occur frequently in lab and field populations of G. integer (Sakuluk and Cade 1980) mole crickets S. acletus and S. vicinus (Ulagaraj 1975), short-tailed crickets, Anurogryllus arboreus (Walker 1979), Oecanthus sp. and the house cricket, A. domesticus (Bell 1979a).

Multiple matings may be of advantage to the females if they provide sperm for fertilizing additional eggs (Gerber 1973, Sakuluk and Cade 1979) or supply endocrinal or behavioural stimuli that affect the total number of eggs laid (Leopold 1976). In addition, multiple matings may be advantageous if they increase the female's life expectancy (Prokopi and Econopolous 1975). Increased genetic diversity in the progeny (Richmond and Ehrman 1974) and material benefits offered to the female (Alcock et al. 1977, Bell 1979, Thornhill 1976a, 1979) associated with multiple matings make them beneficial to the female.

Males gain in multiple mating with a female in that they may realize increased reproductive success. However, several costs are associated with multiple matings. For instance, such costs may involve increased time and energy courting and possibly provisioning the female (Parker 1970b). Females may suffer by having reduced time available for eating or ovipositing (Walker 1980).

Mating Behaviour and Population Density

Spacing patterns are of considerable importance in the study of social behaviour of animals (Brown and Orians 1971). In species where one sex is free of parental investment, energy is often allocated to intrasexual competition for resources and mates, especially if such resources are unevenly distributed (Emlen and Oring 1977). Lek formation is characteristic in species where males are emancipated from parental investment, and clusters of males may increase the number of females attracted per male (Alexander 1975, Bradbury 1981). Territorial behaviour, or site dependent displays that result in conspicuousness or avoidance (Otte and Joern 1975) is thought to be important in spacing males. In crickets, the male calling song serves this function (Cade 1979a, 1981b). In addition, clusters of male crickets probably increase the intensity of the signal at the source such that the acoustical field increases in size and continuity through time and space (Bradbury 1981) even though an individual may decrease his song production at high densities (Alexander 1961).

It has been hypothesized that leks may be of advantage to the males in their achieving more matings on average, than if they remained solitary, this might result if females prefer aggregated males (Alexander 1975, Bradbury 1981). Cade (1981b) found that significantly more female G. integer were attracted to aggregations in loudspeaker treatments, than isolates. Morris et al. (1978) demonstrated that female katydids Conocephalus nigropleurum prefer a loudspeaker playing two male songs over a single male song in the laboratory. Female preference for aggregated males may allow females to examine large numbers of males in the least time possible and assess areas of maximum accessibility (Bradbury

1981). Furthermore, females may be capable of assessing mate choice of other females and gain more information about the male (Bradbury 1981). Females may mate more readily if males are more common (Alexander 1975).

Reduced predation pressures have been suggested to be important in lek formation (Lack 1968); however, this hypothesis has received little experimental support. Indeed, Cade (1979b) found aggregated and isolated loudspeakers, emitting male calling song, did not differ in the likelihood of attracting parasitic flies.

Much of the literature on density effects deals with alterations in the sex ratio. Often density and sex ratio are related phenomenon. Emlen and Oring (1977) suggested that the operational sex ratio (the average ratio of sexually active males to fertilizable females) is of critical importance in analyzing and interpreting social systems.

Information on differences in survival, growth rates, reproductive rates and aggression between densities and at different sex ratios have been examined in a variety of taxa.

Density increases have been shown to increase maturation time in the house cricket, A. domesticus, (McFarlane 1966). Increased density also decreases the mean individual weight in crickets, A. domesticus, and aphids, Drepansiphum platanoides, (Dixon 1975) and the locust, Schistocerca pallens, (Antoniou 1978). Increased density decreases the mean percent survivorship in A. domesticus (Tennis et al. 1979) and the corn earnworm, Heliothes zea, (Burton 1969).

Increased population density may result in increased aggression in crayfish if resources are limiting (Bovjberg and Stephan 1971). In low densities, dominant males gain a mating

advantage in the cockroach Eublaberus posticus; however, such advantages are lost at higher densities because dominant males are reluctant to leave defended refugia (Gorton et al. 1979). Alexander (1961) suggested that aggression is reduced at high density populations of field crickets and males become more tolerant of each other.

There is some confusion as to the effects of population density on mating frequency since most authors either do not consider mating rates of each sex, or the duration during which observations were performed and/or techniques used render studies incomparable. Mating rates of the fly, Drosophila melanogaster, were found to be higher in normal densities than high density populations (Jacobs 1950). Eckstrand and Seiger (1975) and Spiess and Spiess (1968) found that increased densities of D. pseudoobscuraand D. persimilis, respectively, increased the amount of mating within 30 minutes and decreased the time until the first mating. In the corn earworm, Heliothes virescens, (Jones et al. 1979) and H. zea (Burton 1969) mating frequency decreased as density increased. In the mealworm, Tenebrio moliter, crowding increased mating to a limit after which copulation was inhibited (Gerber 1973). In the Indian meal moth, Plodia interpunctella, individuals maintained at a one to one sex ratio at different densities did not experience any differences in female mating frequency (Brower 1975). However, if the number of females was increased the average number of matings per female increased in the Indian meal moth (Brower 1975) and the coddling moth, Carpocapsa pomonella (Howell et al. 1978).

Much of the work relating to density centres on female fertility at various densities. Crowding increases the percent of

egg hatch in Schistocerca pallens (Antoniou 1978), however this is an exception. In Dendroctonas bark beetles, females oviposit more eggs at low population densities (Coulson 1979). Egg production decreases at high densities of the corn earnworm, H. zea (Jones et al. 1975) and H. antiqua (Robinson and Zurlini 1979), the grasshopper, Orinthoacris turbida (Antoniou 1973), and the grasshopper, Humbe tenuicornis (Antoniou 1978). Increased egg production in these species may be due to their increased longevity at the low densities (Antoniou 1978).

In crickets, some effects of density have been noted. At high densities male movement is increased. Other characteristics found in males at the low density, such as territoriality, calling song and aggressiveness, are reduced (Alexander 1961). Cade (1979a) found that males often adopt silent searching behaviours when an area is occupied by calling males or there are taped recordings of the male calling song. Otte and Joern (1975) found that densities of the grasshopper Ligurotettix coquilletti were maintained by territorial spacing of males. They proposed that the number of females inseminated by males successful in defending an area will initially increase as the density of males increases, but at some point the cost of defense will become too great in terms of time and energy. At this point their model agrees with Alexanders' (1961) prediction that aggressive behaviour will decrease as density increases. The effects of density on female behaviour has not been observed in crickets before.

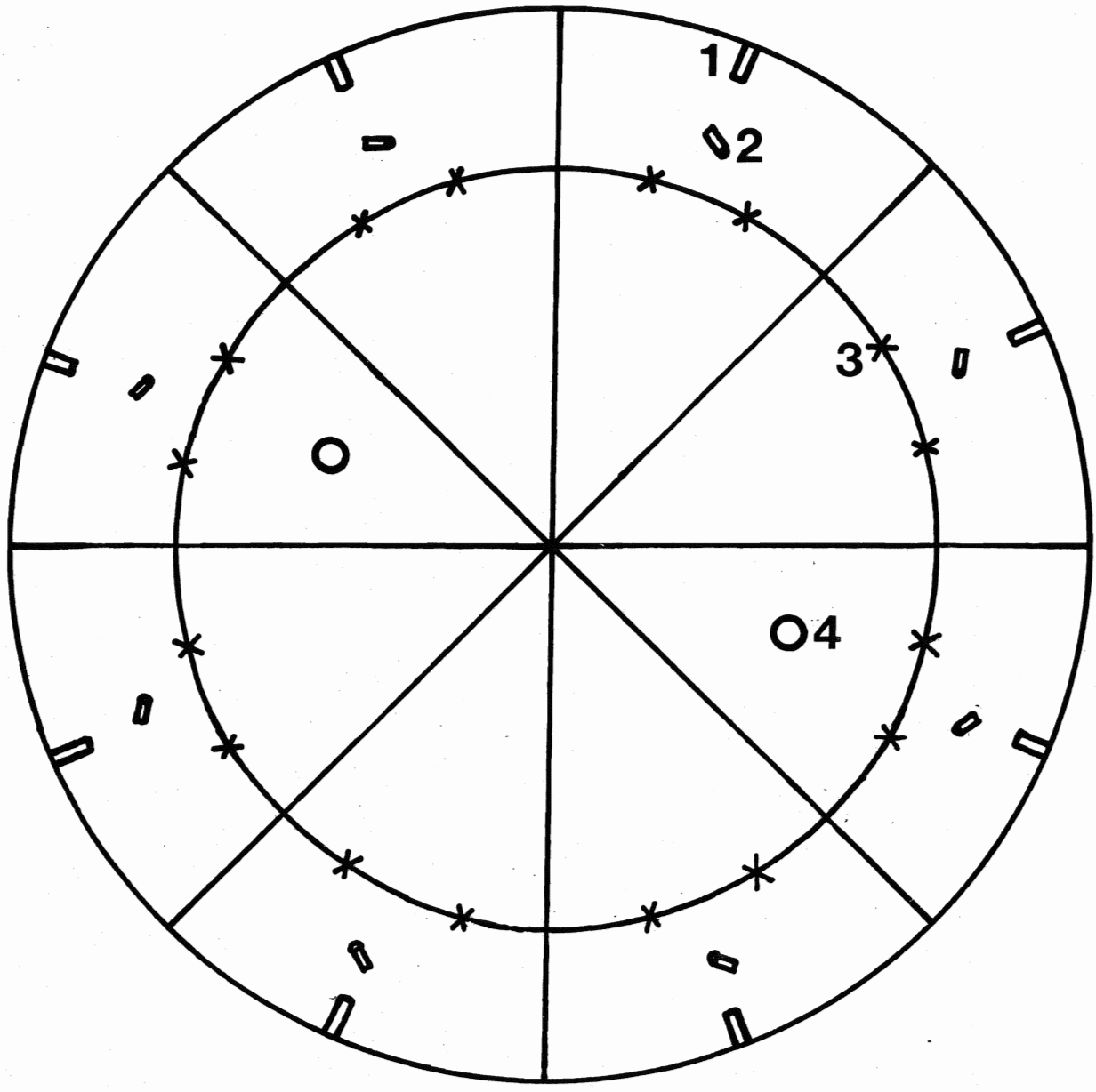
METHODS

Captive Conditions

Wild Gryllus integer were captured in Texas and cultured in the laboratory. Crickets were placed on a 12L:12D photoperiod in 17-gallon trash cans until they neared the last instar. They were then placed in screened terraria under heat lamps and put on a 17L:7D overhead fluorescent photoperiod. Newly eclosed adults were removed daily and placed in individual glass holding jars. Adults were marked distinctively on the thorax and/or femur with Corrector Liquid Paper ®. Males and females were weighed on a Mettler Balance, usually within five days of their adult molt. The observations were conducted in two circular galvanized steel arenas (2.45 m in diameter, Fig. 1). The bottoms of the arenas were lined with sheet plastic and covered with a mix of vermiculite and sand. The arenas were moistened daily. One arena, 0.3 m high, was illuminated with three, 25 watt incandescent red light bulbs suspended 0.5 m above the substrate. The other was 0.9 m high and illuminated with four red lights suspended above the substrate. Each arena was divided into eight equal area sections with string placed above the substrate. Each of these sections was divided into six subsections with marker flags. A wooden block (15 x 4 x 4 cm) and cotton-stoppered vial of water were placed in the eight major sections. Food (Purina cat chow) was placed in two opposing sections. Overhead lights were placed on a 17L:7D photoperiod.

Figure 1

A diagram of the indoor arena used to observe crickets *Gryllus integer* with marked locations of 1. wooden blocks 2. water vials 3. boundary flags 4. food dishes.



SCALE

6.5 cm = 1 m

Observations

Two treatments of male densities were created and will hereafter be referred to as the low (six males and six females) and high (twelve males and six females) density populations. Baseline data on diel patterns of calling, courting and mating were obtained through continuous observations over 30 h on a low density population. Additional data collected on a high density population over 27 days were used to establish techniques and to study mating frequency as individuals aged.

Observations were performed in seven hour blocks during the dark hours between 2 February and 14 August 1980. A total of 680 h of observation were included. In each trial the cohort of individually marked males was introduced first into the arena. Six virgin females, usually less than three days of adult age, were introduced into the arena 36 hours later. Females generally were removed by day 18 of adult age. In all but one case in which a low density population was observed independent of a high density counterpart, paired runs of low and high density populations were initiated within 10 days of each other to reduce seasonal bias (Appendix Table 1). Four sets of replicate experiments were performed at the high density and five replicates at the low density. Replicate experiments within each density were pooled for statistical analysis. To reduce arena bias (substrate or lighting differences), population densities were alternated between arenas.

The number of hours an individual was observed varied within and between trials. Therefore, mean hourly behaviour

rates for each individual were calculated. The duration of calling and courting behaviour (i.e. song production) of each male was timed to the nearest second. Calling and courting rates were determined as the mean number of minutes per hour an individual male spent performing the behaviour. Rates of the durations females were courted were also determined. The identity of individual males involved in a fight, the outcome, duration and location were recorded. The male who retreated was considered the loser. Individual rates of fighting were determined by calculating the mean number of fights per hour observed. Rates of the number of fights an individual won per hour were also obtained, as was the percentage of fights an individual won per hour (regardless of the total time observed). The position of individuals within the 48 equal area sections was routinely recorded at thirty minute intervals. Individual rates of movement were estimated as the mean number of section changes per hour observed.

In a successful mating, a female climbed on a male's back and, with her bursa copulatorix, accepted and retained a spermatophore passed by the male. For each mating, the time and location of the mating and the identity of the participants were recorded. By inspecting mated females at two minute intervals, the duration a spermatophore was retained, and its fate, were identified and recorded. Post-copulatory guarding was operationally defined by a male antennating or remaining within 10 cm of the female. The duration of guarding was timed.

Statistical Analyses

Homogeneity of variances was determined with a Bartlett's test (Sokal and Rohlf 1969). Mann-Whitney U-tests were used to determine differences in the mean rates of behaviours between densities (Sokal and Rohlf 1969). Means are accompanied by standard error unless otherwise stated. Chi-square tests were used to determine whether the frequency of observed behaviours differed significantly from expected values. Two by two contingency tables with Yates correction were used to compare frequencies of behaviours between densities. Data sets were log transformed (in (N+1)) to approximate a normal distribution prior to testing with a parametric One-way Analysis of Variance (ANOVA). Data which yielded significant ANOVA values were subsequently tested with linear, logarithmic, exponential and power regressions (Sokal and Rohlf 1969). The most significant fits are described. If all regression fits were non-significant, then the GT2-method for multiple comparisons among pairs of means was used to test differences (Sokal and Rohlf 1969).

RESULTS

Results concerning the reproductive behaviour of male and female G. integer at two male densities are now described. Results which are baseline in nature are included in the appendices. Data comparing behaviours of individuals within and between densities are presented in tables and graphs which accompany this section.

Diel Periodicity

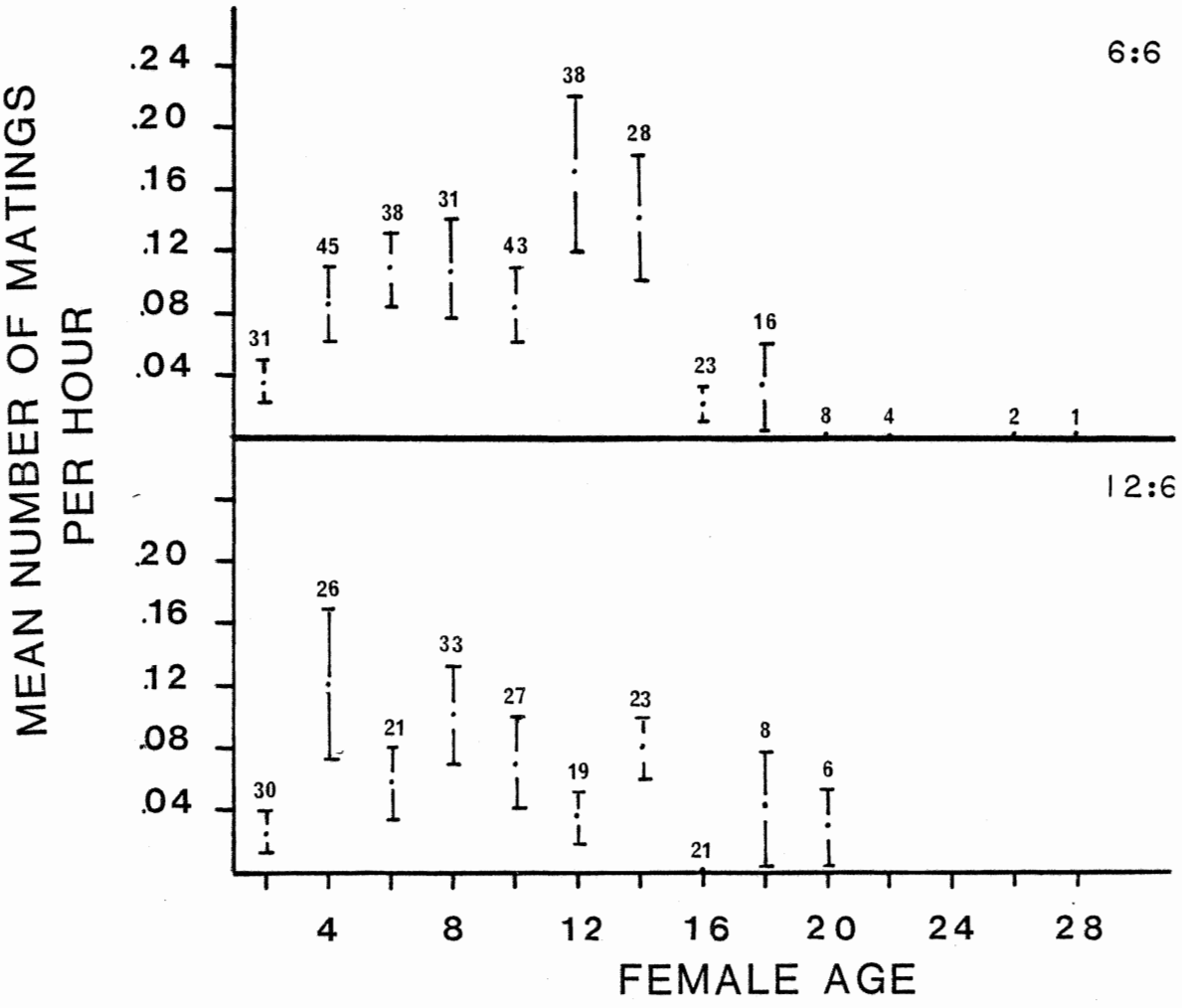
Thirty hours of continuous observations were conducted on a low density population to establish rates of mating, calling and courting behaviour over 17 hours of light and 13 hours of dark. The mean number of matings per male occurring each hour during this period are in Appendix Fig. 1. The mean hourly number of matings did not vary significantly over this 30 h period (ANOVA, $F=0.864, p > 0.05$). The mean number of minutes males courted per hour (Appendix Fig. 2) did not vary significantly over 30 h ($F=0.477, p > 0.05$). However, the mean number of minutes males called per hour (Appendix Fig. 3) did vary significantly during this period ($F=2.89, p < 0.05$) with more calling occurring during the dark hours.

Age

There were no significant differences between densities in the ages during which males (Mann-Whitney U-test, $Z=0.52$, $p=0.302$) and females ($Z=0.487, p=0.312$) were observed (Appendix Table 2). Female mating rates are shown as a function of age in Fig. 2. The baseline data indicated that female mating

Figure 2

The mean number of matings per hour (with standard errors) by females as they aged at low (six males and six females) and high (twelve males and six females) densities. The numbers above the standard error bars represent the number of females used to calculate the means.


MEAN NUMBER OF MATINGS PER HOUR
.24
.20
.16
.12
.08
.04
6:6
31
45
38
31
43
38
28
23
16
8
4
2
1
12:6
.20
.16
.12
.08
.04
30
26
21
33
27
19
23
21
8
6
4
8
12
16
20
24
28
FEMALE AGE

rates were reduced after 18 days of adult age (Appendix Table 3). The mean mating rates of females did not vary significantly with age in the low ($F=1.75, p > 0.05$) or high density ($F=1.55, p > 0.05$). Mean male mating rates did not vary significantly with age at the low ($F=0.985, p > 0.05$) or high density ($F=0.925, p > 0.05$). (Fig. 3).

Male and female mating rates were analyzed according to the date since trial initiation at both densities to ensure that mating rates were similar throughout the duration of the experiments (Appendix Figs. 4,5). Mean male mating rates did not vary significantly over the days following trial initiation at the low ($F=1.44, p > 0.05$) or high density ($F=1.10, p > 0.05$). Mean female mating rates also did not vary significantly over the days following trial initiation at the low ($F=1.14, p > 0.05$) or high ($F=0.847, p > 0.05$) density.

Density

Replicate trials within each density were combined for statistical analyses. The mean number of matings per hour by males and females in each replicate trial are in Table 1. There were no significant differences between the variances in mean female mating rates within the low (Bartlett's test, $X^2=9.63, p > 0.05$) or within the high density replicate trials ($X^2=5.74, p > 0.05$). In addition there were no significant differences between the variances in mean male mating rates within the low ($X^2=7.68, p > 0.05$) or within the high density replicate trials ($X^2=6.03, p > 0.05$).

Figure 3

The mean number of matings per hour (with standard errors) by males as they aged at low (six males and six females) and high (twelve males and six females) densities. The numbers above the standard error bars represent the number of males used to calculate the means.

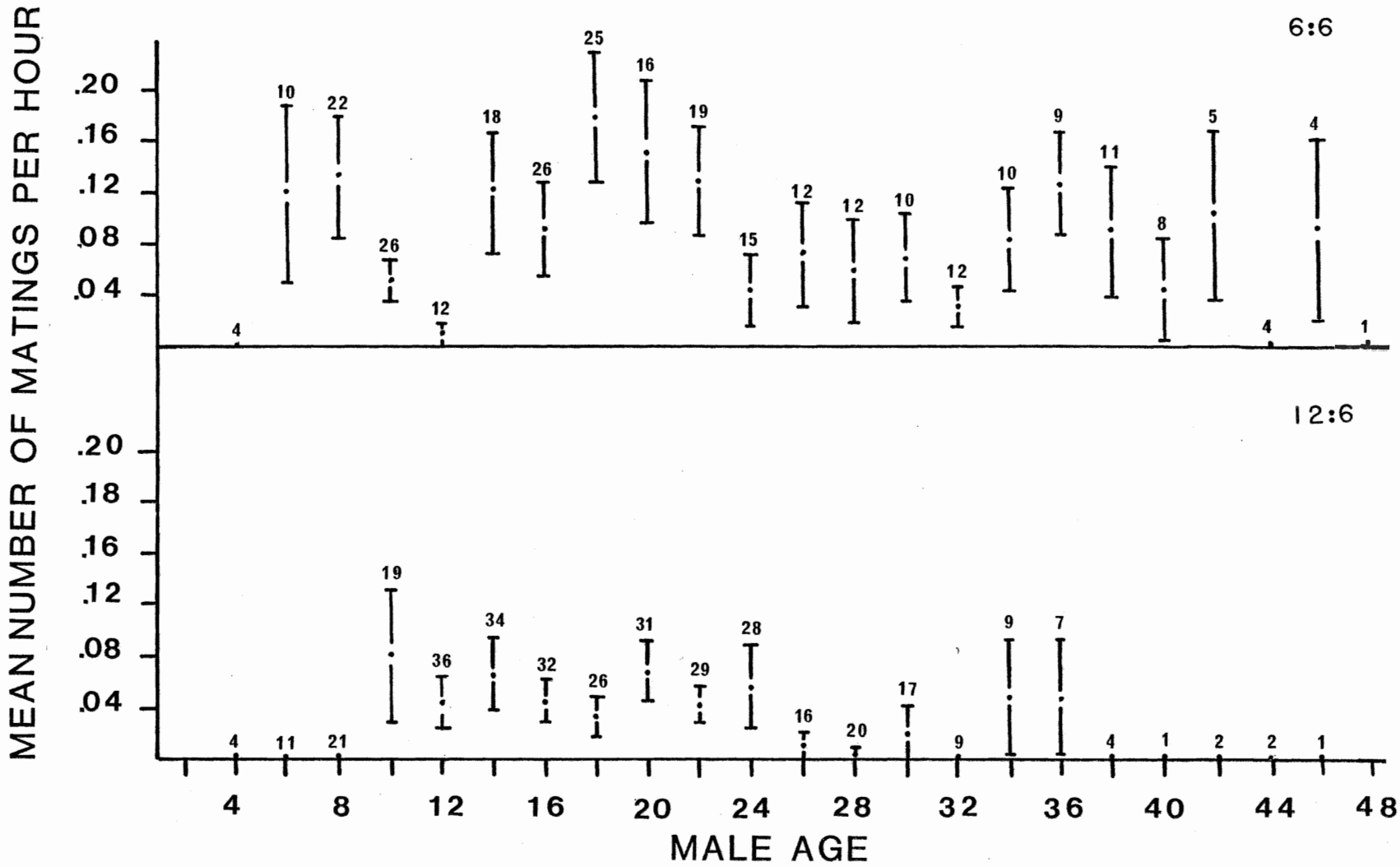

6:6
12:6
MEAN NUMBER OF MATINGS PER HOUR
.20
.16
.12
.08
.04
.20
.18
.16
.12
.08
.04
4 10 22 26 12 18 26 25 16 19 15 12 12 10 12 10 9 11 8 5 4 4 1
4 11 21 19 36 34 32 26 31 29 28 16 20 17 9 9 7 4 1 2 2 1
4 8 12 16 20 24 28 32 36 40 44 48
MALE AGE

Table 1: The mean number of matings per hour by male and female crickets, (G. integer), in replicate trials at low (six males and six females) and high (twelve males and six females) densities.

		Males				Females		
Density	Run	n	Mean Mating Rate	SD	S^2	n	Mean Mating Rate	SD	S^2
Low	1	10	.048	.058	.0033	13	.061	.0687	.0047
	2	8	.020	.036	.0013	6	.027	.0223	.0005
	3	11	.059	.047	.0022	13	.048	.0656	.0043
	4	7	.144	.109	.0129	6	.171	.0922	.0085
	5	9	.080	.070	.0049	9	.068	.0949	.0090
total		45	.067	.077	.0059	47	.069	.0839	.0070
High	1	16	.024	.035	.0012	7	.045	.053	.0028
	2	15	.030	.04	.0016	10	.043	.047	.0022
	3	22	.162	.029	.0009	11	.039	.048	.0023
	4	17	.050	.051	.0026	9	.097	.091	.0084
total		70	.031	.044	.0019	37	.055	.067	.0044

One objective of these experiments was to determine if females are stimulated to mate more often when males are more numerous. Frequency distributions of female mating rates at both densities are in Fig. 4. There were no significant differences between the mean mating rates of females in the low ($\bar{X}$=0.069±0.012) and high ($\bar{X}$=0.055±0.011) densities (U-test, Z=0.646,p=0.258). Thirty percent of the females at the low density (N=47) and 46 percent of those at the high density (N=37) never mated during the hours observed. The ratio of mated to non-mated females was not significantly different between densities (2x2 χ^2_y=0.40,p > 0.05). Variances in female mating rates at the low density were significantly greater than at the high density (Bartlett's test, χ^2=14.4,p < 0.01) (Table 1). Frequency distributions of the number of times a female mated in a day are in Figure 5. There were no significant differences in the mean number of times females mated in a day at either density (U-test, Z=1.25,p = 0.105). Females mated with up to three different partners in a single day of observation.

Density effects on the frequency of male mating were also examined. Frequency distributions of male mating rates at both densities are in Figure 6. The mean mating rate of males at the low density ($\bar{X}$=0.067±0.012) was significantly greater than the mean male mating rate at the high density ($\bar{X}$=0.031± 0.005) (U-Test,Z=2.63,p = 0.004). To adjust for sex ratio differences between densities, mating rates of males at the high density were doubled. This adjustment indicated that there were no significant differences in the mean mating rates

Figure 4

Frequency distributions of the mean number of matings per hour by individual females at the low (six males and six females) and high (twelve males and six females) densities.

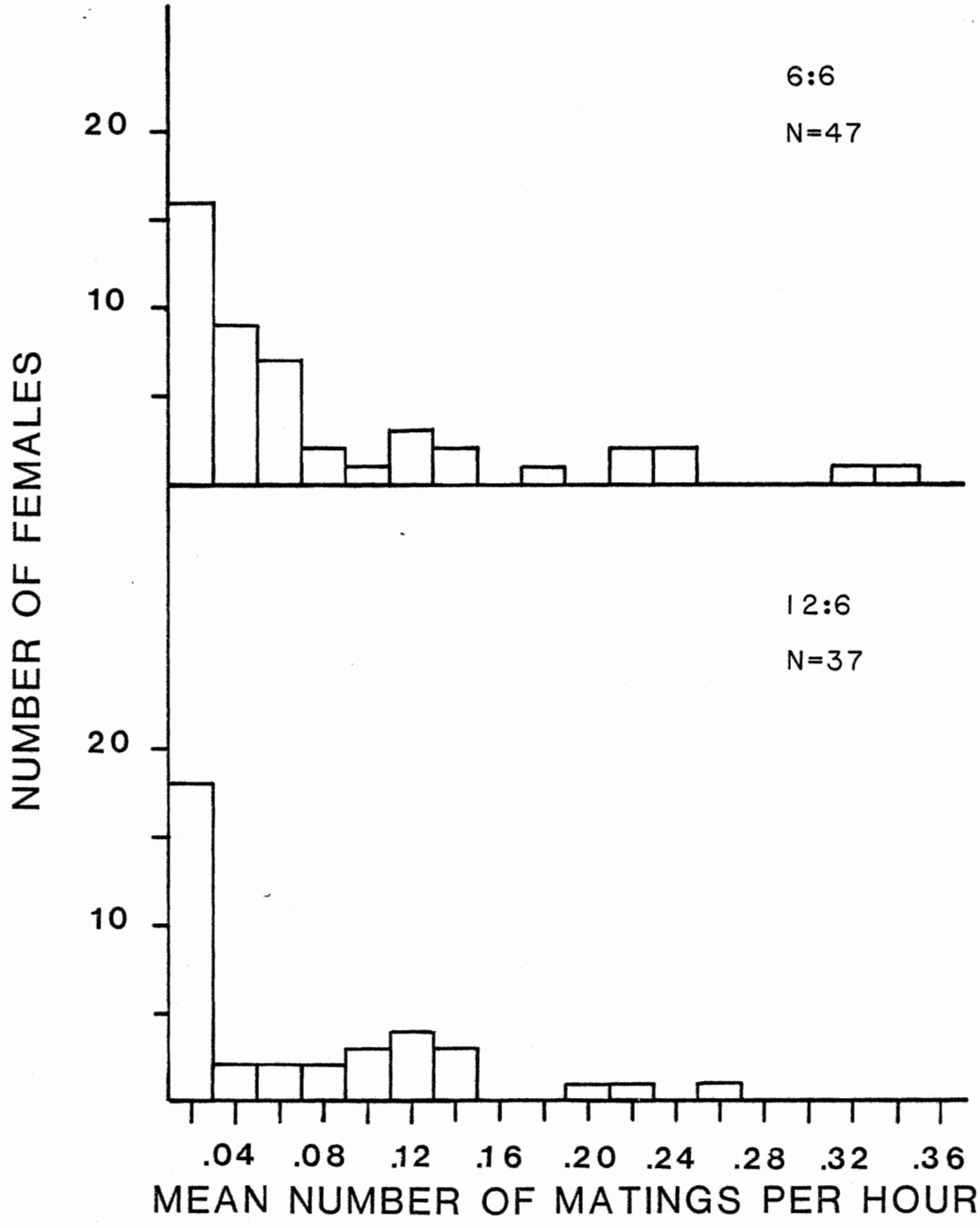

6:6
N=47
20
10
12:6
N=37
20
10
NUMBER OF FEMALES
.04 .08 .12 .16 .20 .24 .28 .32 .36
MEAN NUMBER OF MATINGS PER HOUR

Figure 5

Frequency distributions of the number of times females mated in a day at low (six males and six females) and high (twelve males and six females) densities.

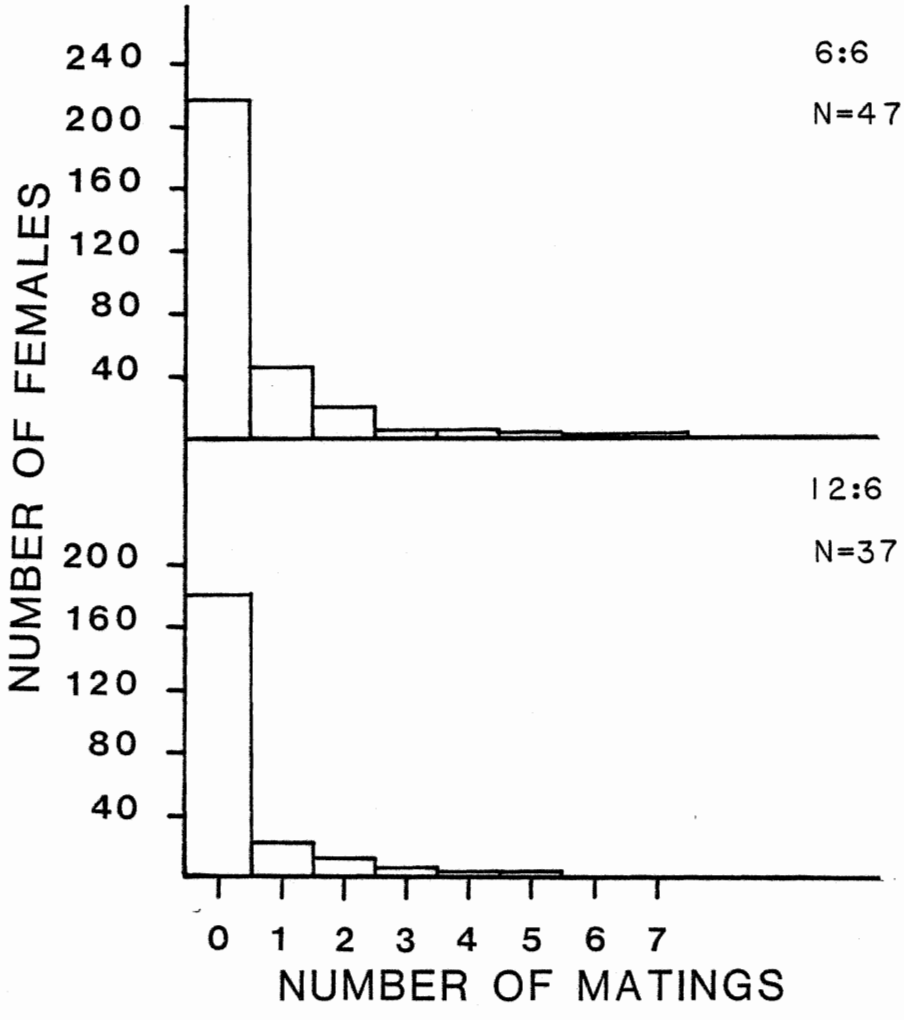
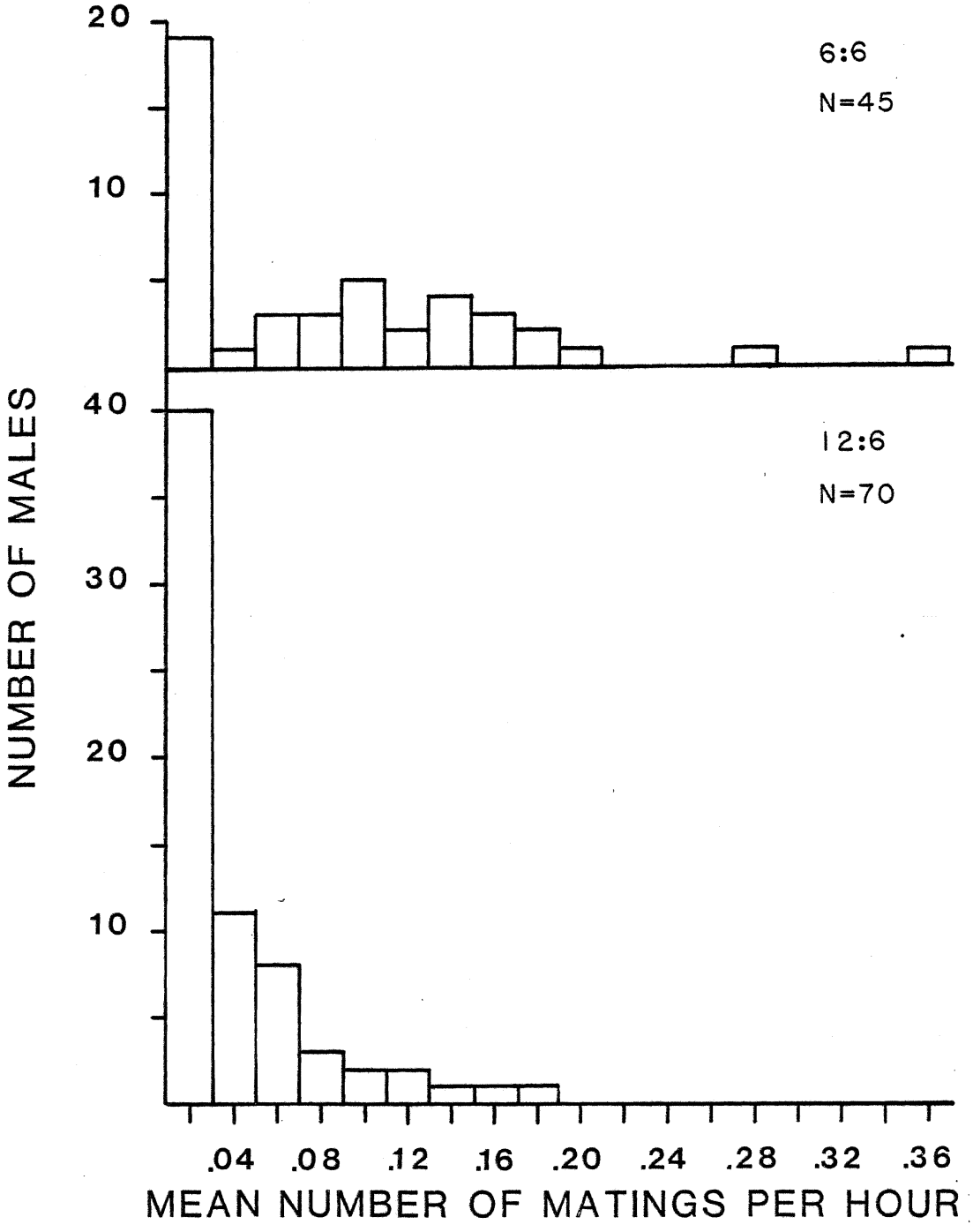

6:6
N=47
12:6
N=37
240
200
160
120
80
40
200
160
120
80
40
NUMBER OF FEMALES
0 1 2 3 4 5 6 7
NUMBER OF MATINGS

Figure 6

Frequency distributions of the mean number of matings per hour by individual males at the low (six males and six females) and high (twelve males and six females) densities.


20
10
6:6
N=45
40
30
20
10
12:6
N=70
NUMBER OF MALES
.04
.08
.12
.16
.20
.24
.28
.32
.36
MEAN NUMBER OF MATINGS PER HOUR

of males at either density (U-test,Z=1.14,p=0.127). Forty percent of the males at the low density (N=45) and 52.9 percent of those at the high density (N=70) never mated during observations. The ratio of non-mated to mated males did not differ significantly between densities (2x2 χ^2y=1.34,p > 0.05). Variances in male mating rates at the low density were significantly greater than variances at the high density (Bartlett's test, X^2=19.27,p < 0.001) (Table 1). Frequency distributions of the number of times males mated in a day at both densities are in Figure 7. Males at the low density mated significantly more often in a day than those at the high density (U-test, Z=4.10,p=0.00003). Males mated with up to three different partners in a day.

As an indirect estimate of reproductive success, male and female mating rates were compared (Table 1). The variances in male and female mating rates were homogeneous at the low density (X^2=0.332,p > 0.05). However, the variance in male mating rates was significantly less than in female mating. rates at the high density (X^2=8.54,p < 0.05).

Movement

The extent to which increased population density influenced individual rates of movement was examined. Frequency distributions of the rates at which males moved are in Fig. 8. There were no significant differences between the rates at which males moved at the low ($\overline{X}$=0.73±0.038) and high densities ($\overline{X}$=0.657±0.035) (U-test,Z=1.44,p = 0.075). Frequency distributions of female rates of movement are in Fig. 9. There were no

Figure 7

Frequency distributions of the number of times males mated in a day at low (six males and six females) and high (twelve males and six females) densities.

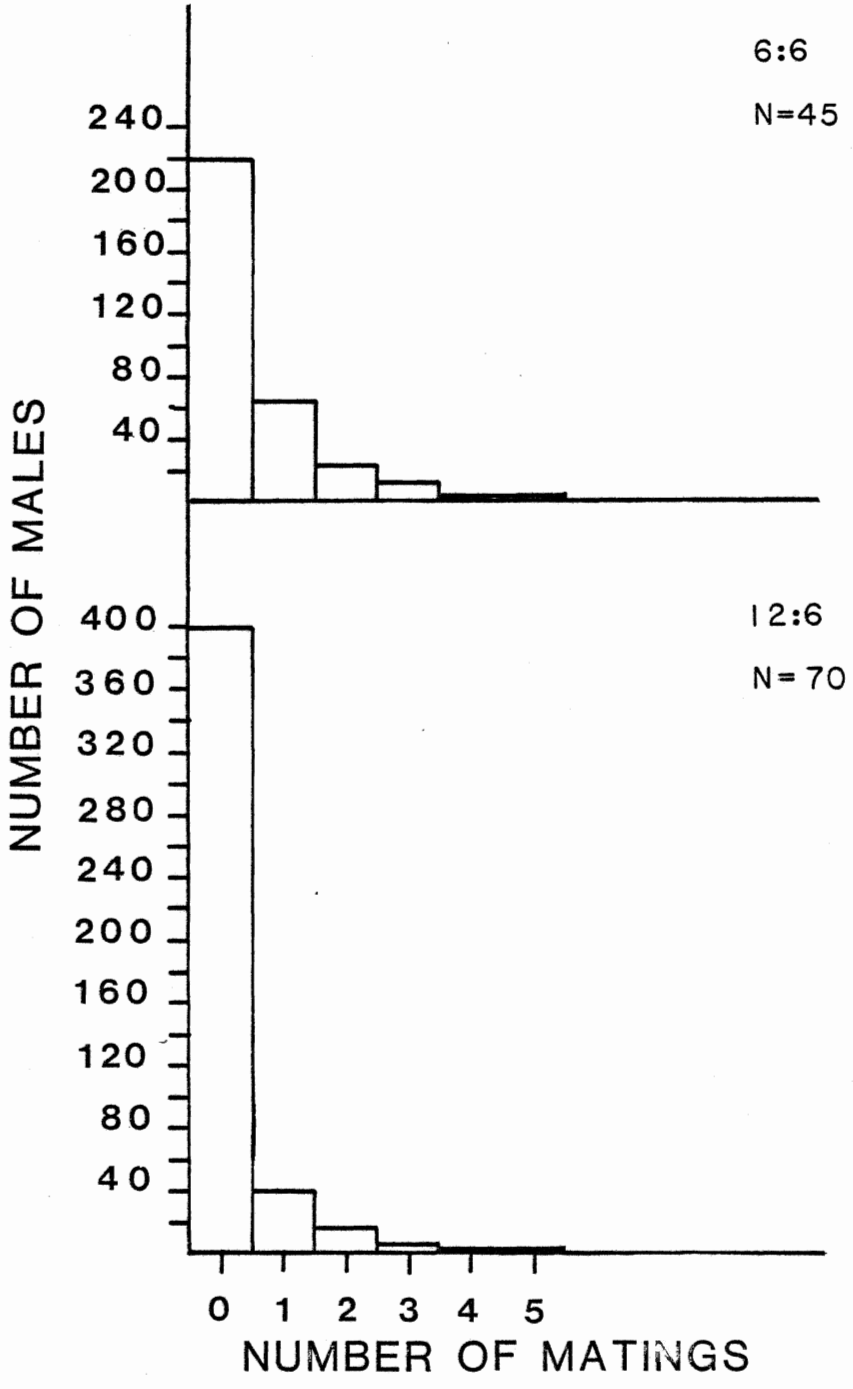

6:6
N=45
240
200
160
120
80
40
12:6
N=70
400
360
320
280
240
200
160
120
80
40
NUMBER OF MALES
0 1 2 3 4 5
NUMBER OF MATINGS

Figure 8

Frequency distributions of the mean number of quadrats males moved per hour, as determined at 30 min intervals, at the low (six males and six females) and high (twelve males and six females) densities.

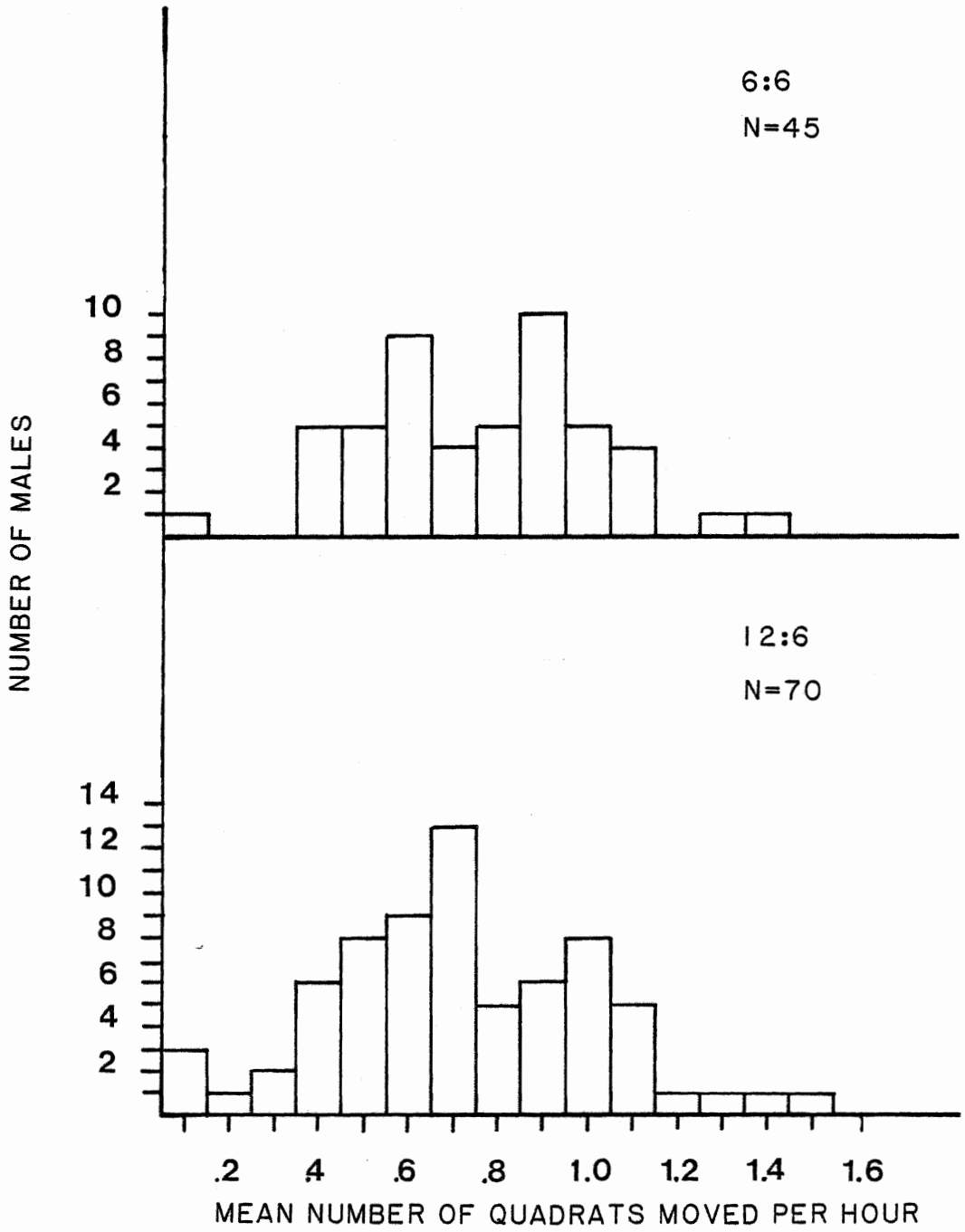
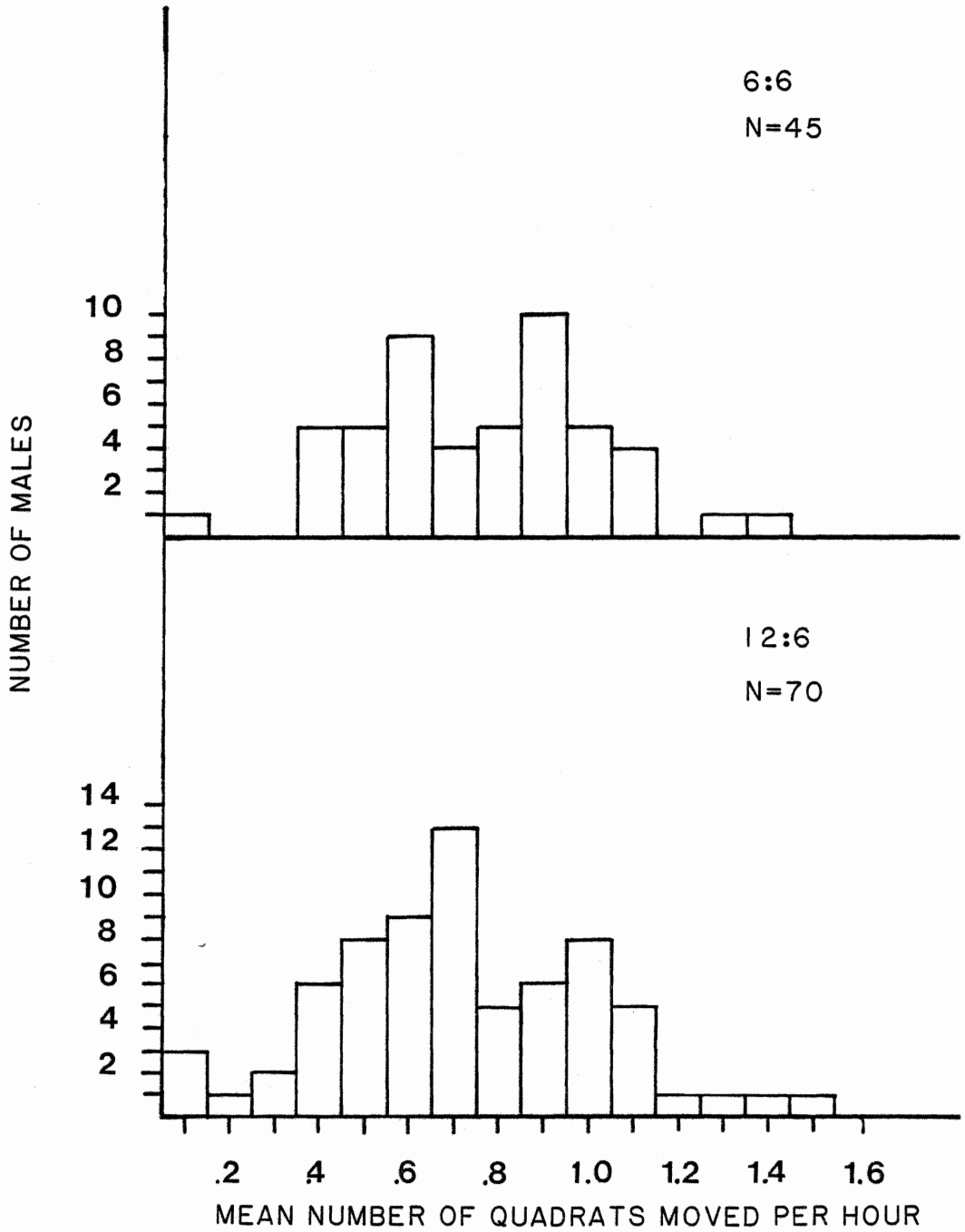

6:6
N=45
10
8
6
4
2
12:6
N=70
14
12
10
8
6
4
2
NUMBER OF MALES
.2
.4
.6
.8
1.0
1.2
1.4
1.6
MEAN NUMBER OF QUADRATS MOVED PER HOUR

Figure 9

Frequency distributions of the mean number of quadrats females moved per hour as determined at 30 min intervals at the low (six males and six females) and high (twelve males and six females) densities.


6:6
N=45
10
8
6
4
2
12:6
N=70
14
12
10
8
6
4
2
NUMBER OF MALES
.2
.4
.6
.8
1.0
1.2
1.4
1.6
MEAN NUMBER OF QUADRATS MOVED PER HOUR

significant differences between the rates of female movement at the low ($\bar{X}$=0.928±0.061) and high densities ($\bar{X}$=0.87±0.51) (Z=0.06,p= 0.476). The mean rates of movement by females were significantly greater than those by males at the low (Z=1.7,p= 0.045) and high densities (Z=3.03,p=0.0012).

Male mating rates did not vary significantly according to their rates of movement at the low ($F=1.27, p > 0.05$) or high density ($F=1.35, p > 0.05$) (Fig. 10). Nor did female mating rates vary significantly with their rates of movement at the low ($F=0.5, p > 0.05$) or high density ($F=1.67, p > 0.05$) (Fig. 11).

Fighting

The mean rates of fighting by males were compared at both densities. Frequency distributions of male fighting rates at the low and high densities are in Fig. 12. The mean rates of fighting per hour at the low density ($\bar{X}$=0.89±0.11) was significantly less than that at the high density ($\bar{X}$=1.32±0.11) (U-test,Z=2.46,p=0.0069). Fighting rates by males at the low density were doubled in order to standardize for the number of males present in both densities and to segregate influences of the sex ratio from those of density. The adjusted mean rates of fighting by males at the low density was significantly greater than that at the high density (U-test,Z=2.01,p=0.022).

The reproductive benefits associated with fighting were also examined at both densities. Male mating rates are shown as a function of their fighting rates in Fig. 13. Mean male mating rates varied significantly according to rates of fighting in the low ($F=4.43, p < 0.05$) but not the high density ($F=1.85, p > 0.05$).

Figure 10

The mean number of matings per hour (with standard errors) by males as a function of the mean number of quadrats moved per hour (with standard errors) as determined at 30 min intervals at the low (six males and six females) and high (twelve males and six females) densities. The small numbers above the standard error bars represent the number of males used to calculate the means.

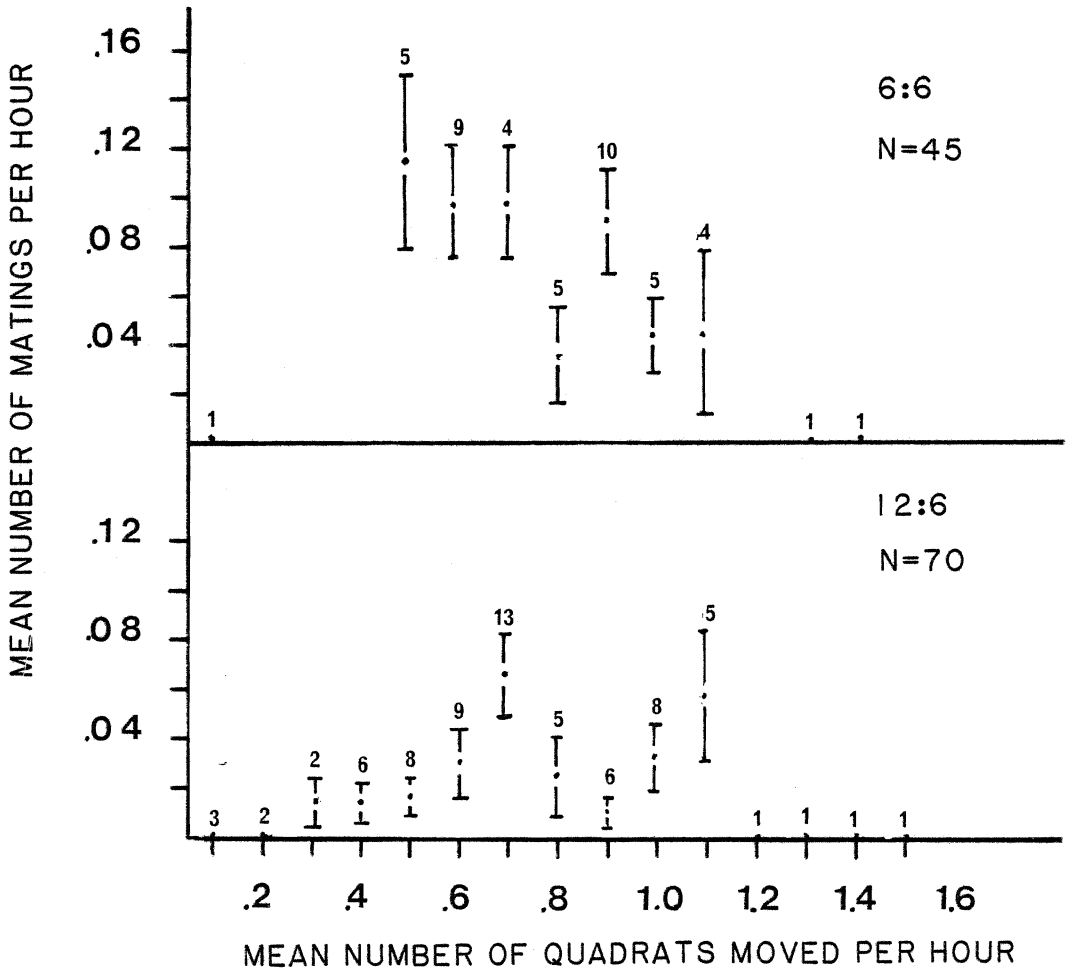

MEAN NUMBER OF MATINGS PER HOUR
.16
.12
.08
.04
6:6
N=45
12:6
N=70
.2
.4
.6
.8
1.0
1.2
1.4
1.6
MEAN NUMBER OF QUADRATS MOVED PER HOUR

Figure 11

The mean number of matings per hour (with standard errors) by females as a function of the mean number of quadrats moved per hour (with standard errors) as determined at 30 min intervals at the low (six males and six females) and high (twelve males and six females) densities. The small numbers above the standard error bars represent the number of females used to calculate the means.

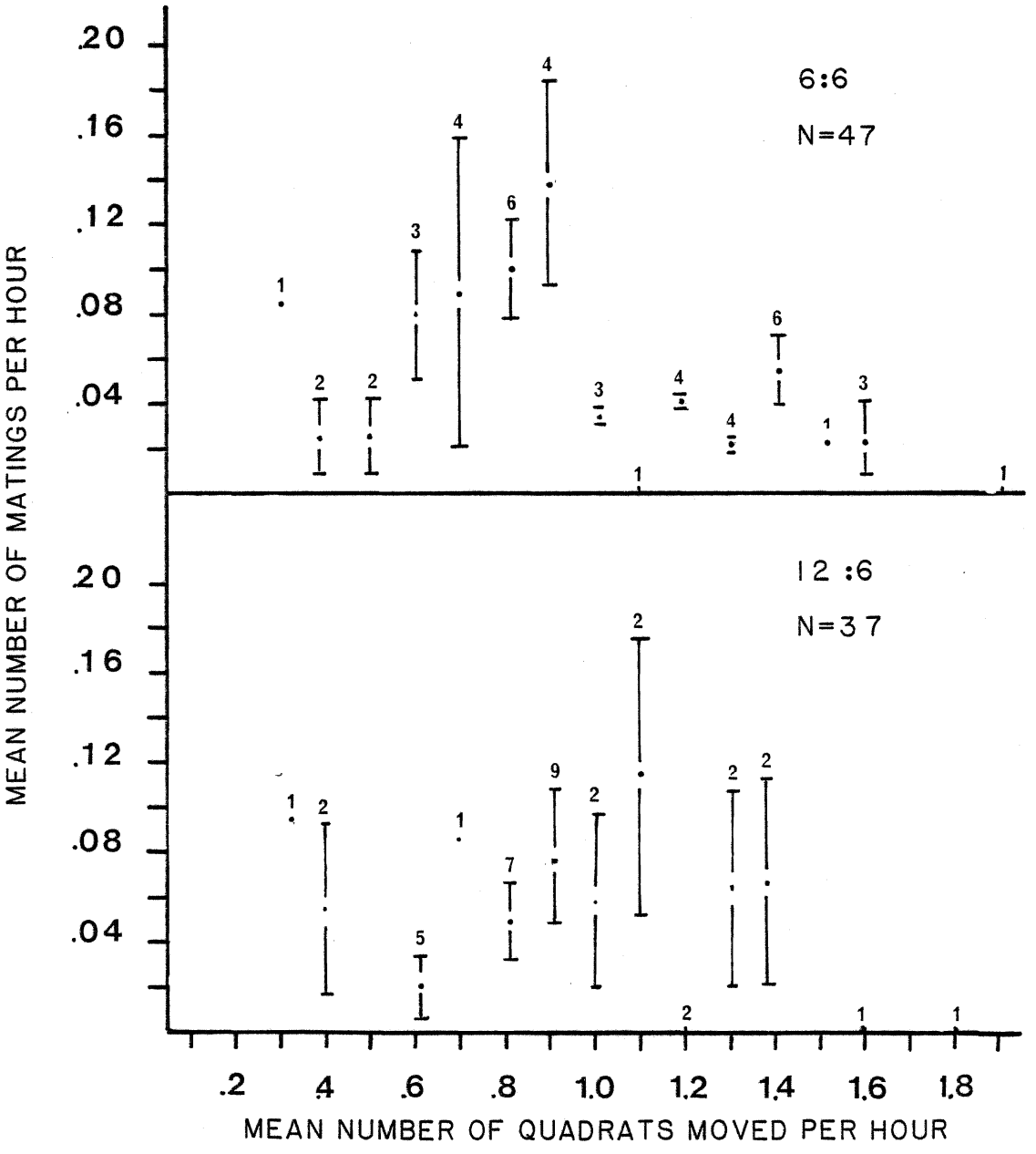

6:6
N=47
12:6
N=37
.20
.16
.12
.08
.04
MEAN NUMBER OF MATINGS PER HOUR
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
MEAN NUMBER OF QUADRATS MOVED PER HOUR

Figure 12

Frequency distributions of the mean number of fights per hour by males at the low (six males and six females) and high (twelve males and six females) densities.

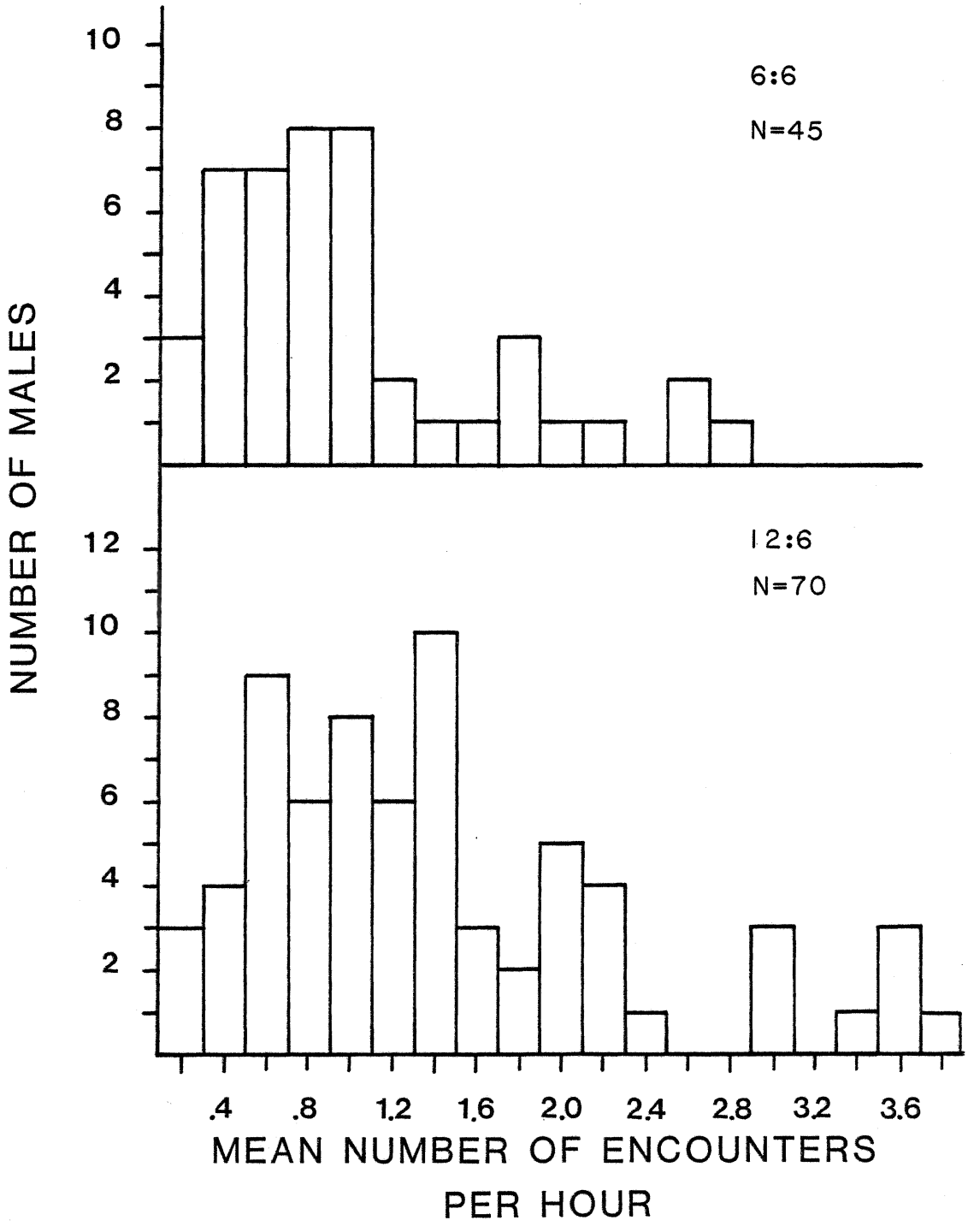
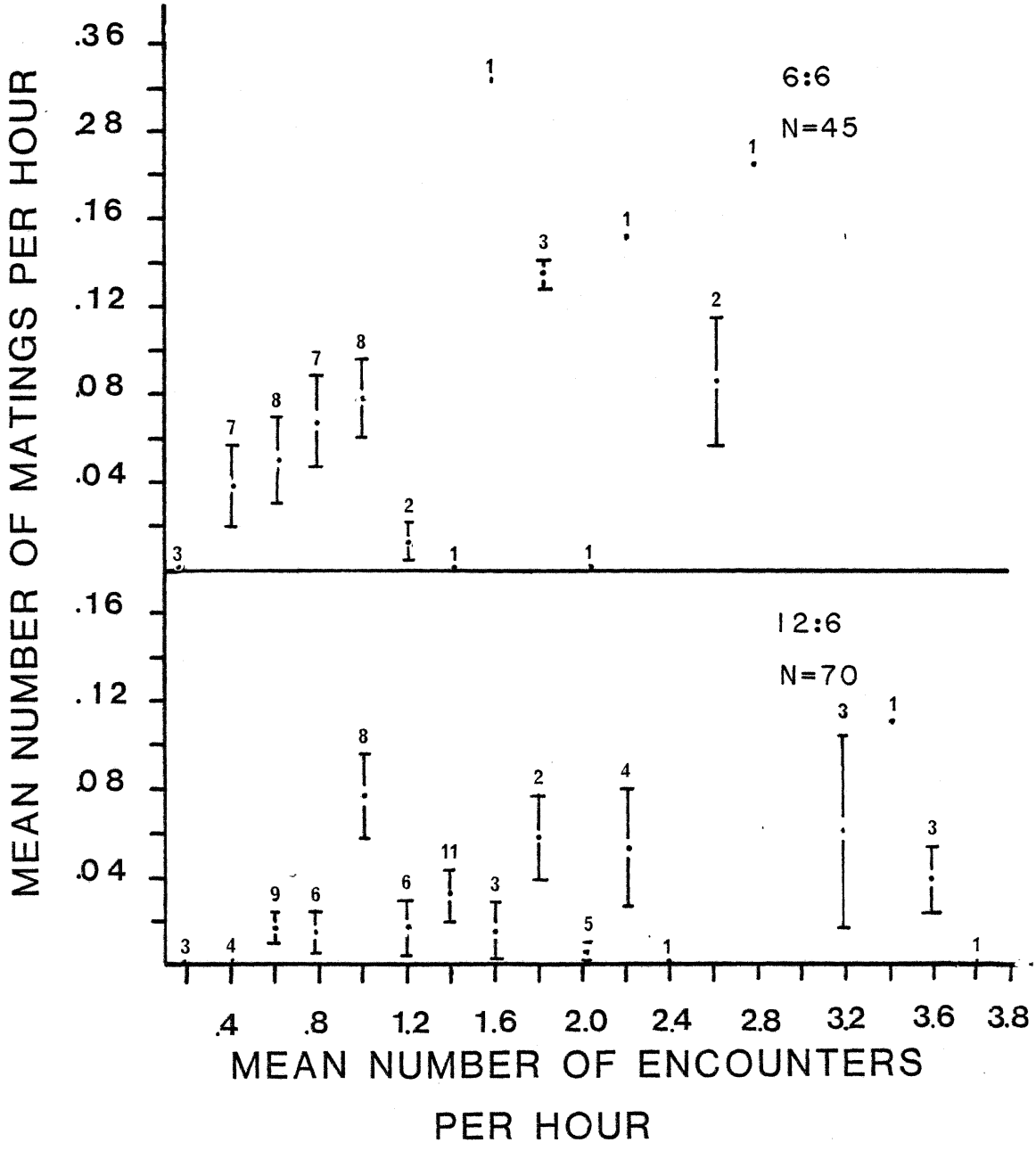

NUMBER OF MALES
10
8
6
4
2
6:6
N=45
12
10
8
6
4
2
12:6
N=70
.4
.8
1.2
1.6
2.0
2.4
2.8
3.2
3.6
MEAN NUMBER OF ENCOUNTERS
PER HOUR

Figure 13

The mean number of matings per hour (with standard errors) by males as a function of the mean number of fights per hour (with standard errors) at the low (six males and six females) and high (twelve males and six females) densities. The small numbers above the standard error bars represent the number of males used to calculate the means.


MEAN NUMBER OF MATINGS PER HOUR
.36
.28
.16
.12
.08
.04
6:6
N=45
12:6
N=70
.16
.12
.08
.04
.4
.8
1.2
1.6
2.0
2.4
2.8
3.2
3.6
3.8
MEAN NUMBER OF ENCOUNTERS
PER HOUR

A power fit was significant at the low density ($r=0.45, p < 0.01$, $Y=0.097(X)+0.007$).

Three approaches were used to determine whether females preferred to mate with dominant males. The number of matings immediately preceded (within 30 min) by fights were examined to determine if females prefer males involved in combat prior to mating and if they subsequently mated with the victors (Table 2). Fights preceded 42.1 percent (N=159) of the matings at the low density and 46.6 percent (N=88) of those at the high density. The victors of such fights mated significantly more often than the defeated male at both the low ($\chi^2=8.12, p < 0.01$) and high density ($\chi^2=7.62, p < 0.01$). Secondly, mating rates of males were examined according to the number of fights they won per hour observed (Fig. 14). Mating rates did not vary significantly with rates of winning at the low ($F=1.51, p > 0.05$) or high density ($F=1.75, p > 0.05$). Finally, mating rates were examined according to the percentage of fights an individual won, independent of the frequency at which the individual fought (Fig. 15). Mating rates varied significantly with the percentage of fights an individual won at the low density ($F=2.95, p < 0.05$) but not at the high density ($F=0.34, p > 0.05$). A power fit was significant at the low density ($r=0.332, p < 0.05, Y=0.016(X)+0.0071$).

The effects of male weight on mating success and fighting abilities were examined at both densities. Frequency distributions of male weights are in Appendix Fig. 6. The mean male weight at the low density ($\bar{X}=462\pm32.1$mg) was not significantly different from that at the high density ($\bar{X}=442.1\pm15.09$mg) (U-test, $Z=1.03, p=0.05$). Male mating rates are shown as a

Table 2: The number of matings immediately preceded (within 30 min) by a fight resulting in a win or loss at the low (six males and six females) and high (twelve males and six females) densities.

Density	Number of Matings Preceded by Fights Resulting a Win	Number of Matings Preceded by Fights Resulting a Loss	Number of Matings Not Preceded by Aggression
Low	50	17	92
High	33	8	47
Total	83	25	139

Figure 14

The mean number of matings per hour (with standard errors) by males as a function of the mean number of fights males won per hour (with standard errors) at the low (six males and six females) and high (twelve males and six females) densities.

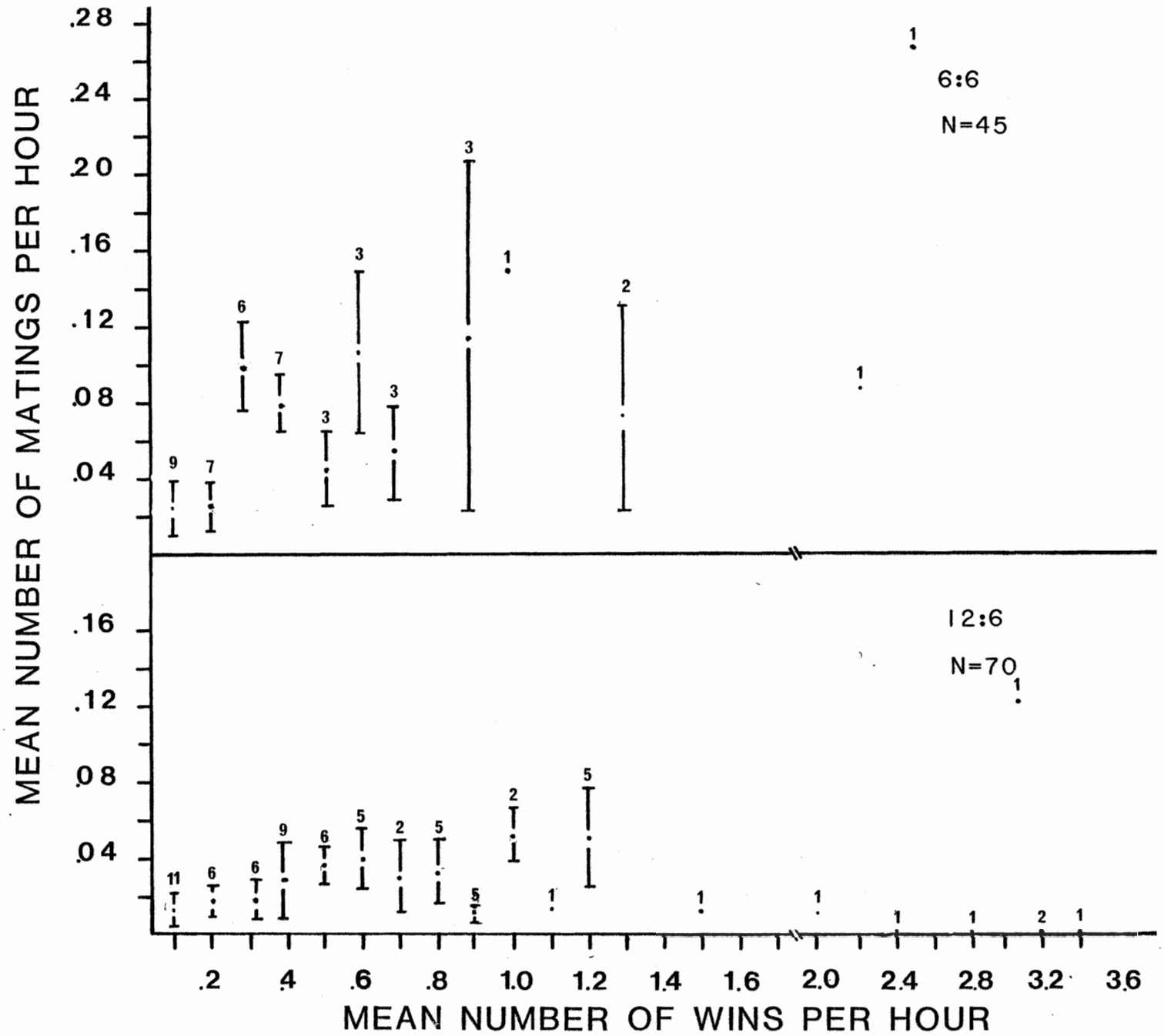
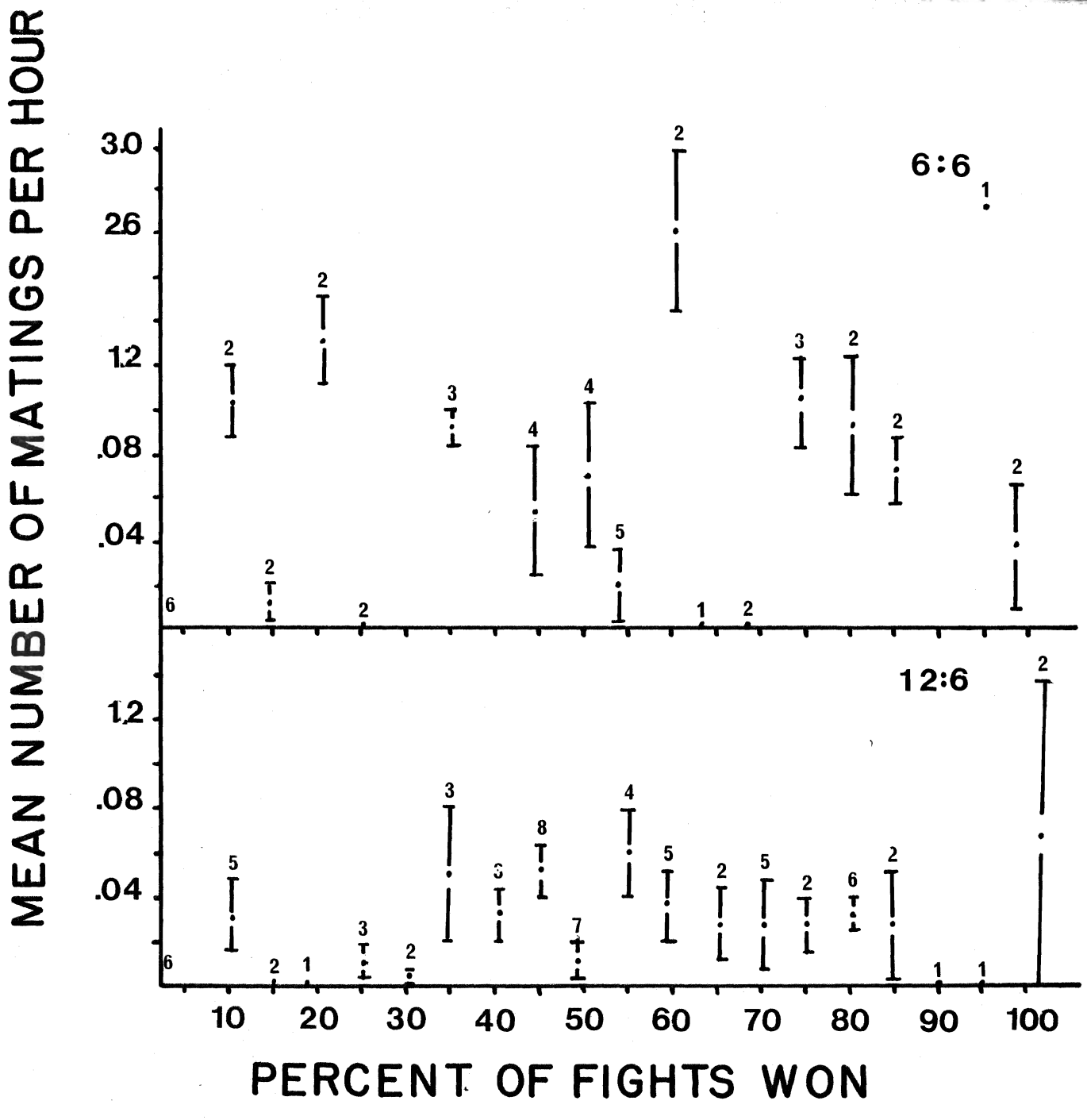

MEAN NUMBER OF MATINGS PER HOUR
.28
.24
.20
.16
.12
.08
.04
6:6
N=45
12:6
N=70
.16
.12
.08
.04
.2
.4
.6
.8
1.0
1.2
1.4
1.6
2.0
2.4
2.8
3.2
3.6
MEAN NUMBER OF WINS PER HOUR

Figure 15

The mean number of matings per hour (with standard errors) by males as a function of the percent of fights a male won at low (six males and six females) and high (twelve males and six females) densities.


MEAN NUMBER OF MATINGS PER HOUR
3.0
2.6
1.2
.08
.04
6:6
12:6
1.2
.08
.04
10
20
30
40
50
60
70
80
90
100
PERCENT OF FIGHTS WON

function of male weight in Fig. 16. Male mating rates varied significantly with weight at the low ($F=3.39, p < 0.05$), but not the high density ($F=0.986, p > 0.05$). There was a significant linear relationship between male mating rates and weight at the low density ($r=0.342, p < 0.05, Y=0.003(X)-0.038$).

Mean rates of fighting by males of different weights are in Fig. 17. Rates of fighting varied according to male weight at the low ($F=3.98, p < 0.05$) but not at the high density ($F=1.71$, $p > 0.05$). There was a significant linear relationship between male weight and fighting at the low density ($r=0.467, p < 0.01$, $Y=0.003(X)-0.361$).

The relationship between male weight and rates of winning were examined (Fig. 18). Rates of winning varied significantly with male weight at the low ($F=3.41, p < 0.05$) and high density ($F.296, p < 0.05$). Male weight was significantly and linearly related to rates of winning at both the low ($r=0.572, p < 0.05$, $Y=0.003(X)-0.89$) and high density ($r=0.47, p < 0.05, Y=0.003(X)-0.6$). The percentage of fights won was also examined according to male weight (Fig. 19). The percentage of fights that an individual won did not vary with male weight at the low ($F=1.01, p > 0.05$) or at the high density ($F=0.93, p > 0.05$).

Song Production

The total duration that males called (for mate attraction and aggression) was measured at both densities. Frequency distributions of male calling rates at both densities are in Fig. 20. The mean male calling rate at the low density

Figure 16

The mean number of matings per hour (with standard errors) as a function of male weight at the low (six males and six females) and high (twelve males and six females) densities.

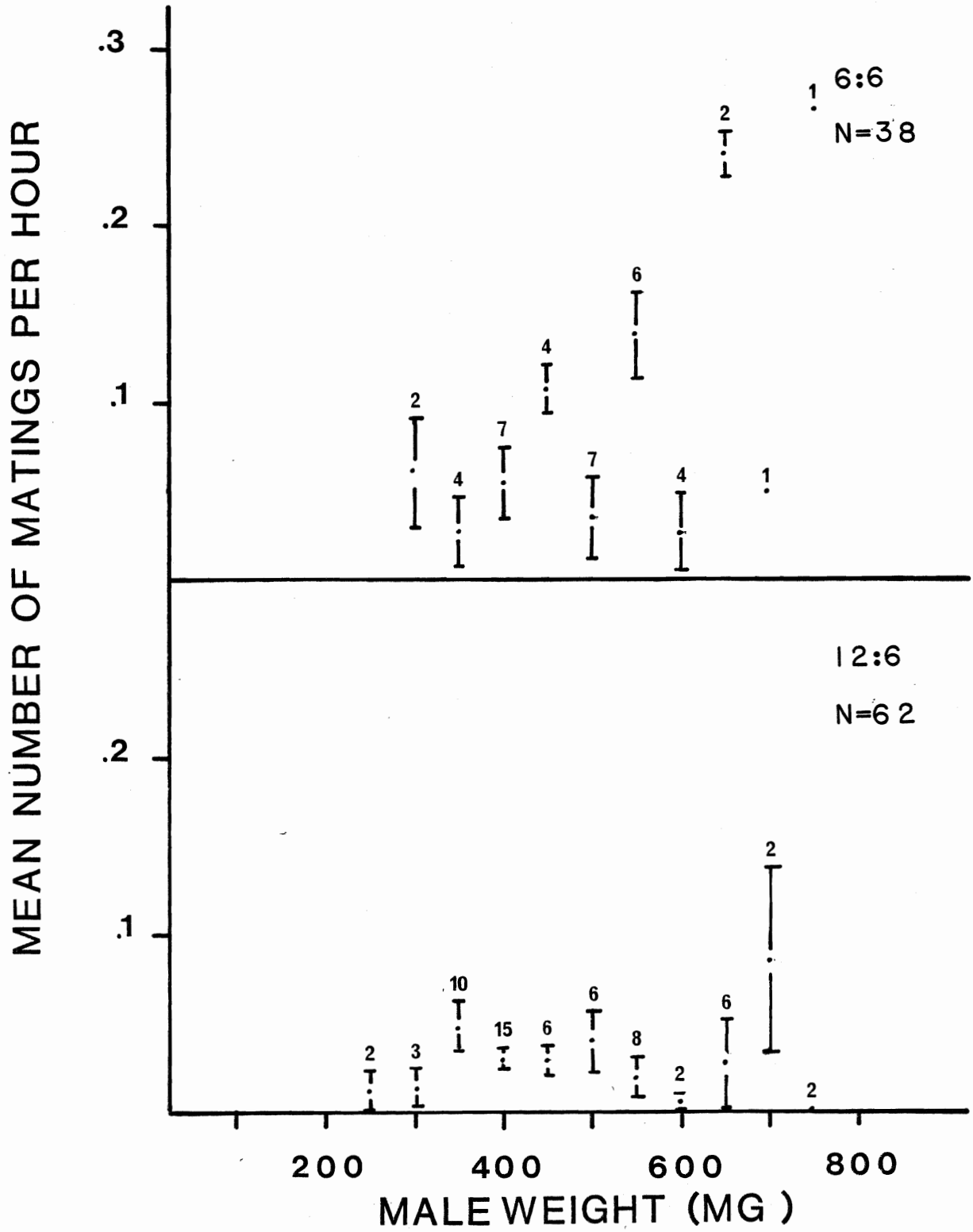

MEAN NUMBER OF MATINGS PER HOUR
.3
.2
.1
6:6
N=38
12:6
N=62
.2
.1
200
400
600
800
MALE WEIGHT (MG)

Figure 17

The mean number of fights per hour (with standard errors) by males of different weights at the low (six males and six females) and high (twelve males and six females) densities.

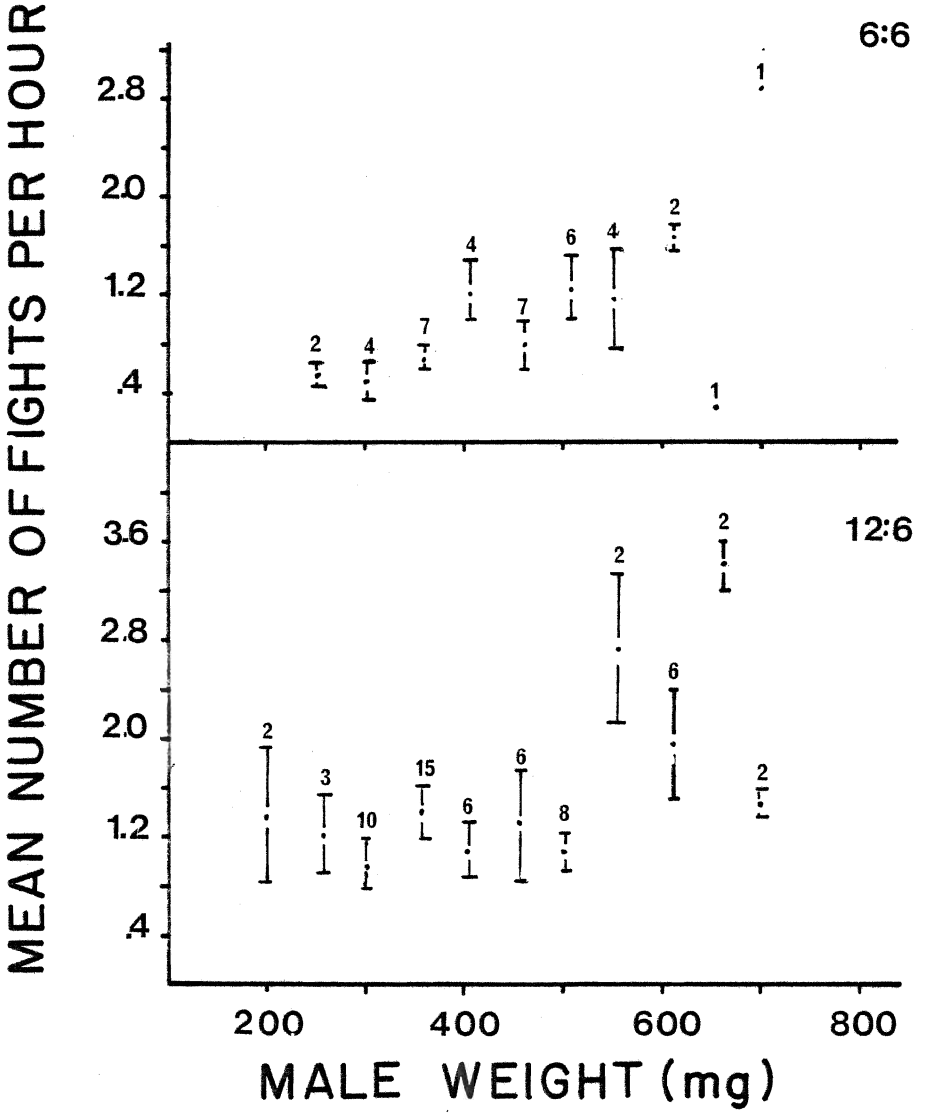

MEAN NUMBER OF FIGHTS PER HOUR
6:6
12:6
2.8
2.0
1.2
.4
3.6
200
400
600
800
MALE WEIGHT (mg)

Figure 18

The mean number of fights a male won per hour (with standard errors) as a function of male weight at the low (six males and six females) and high (twelve males and six females) densities.

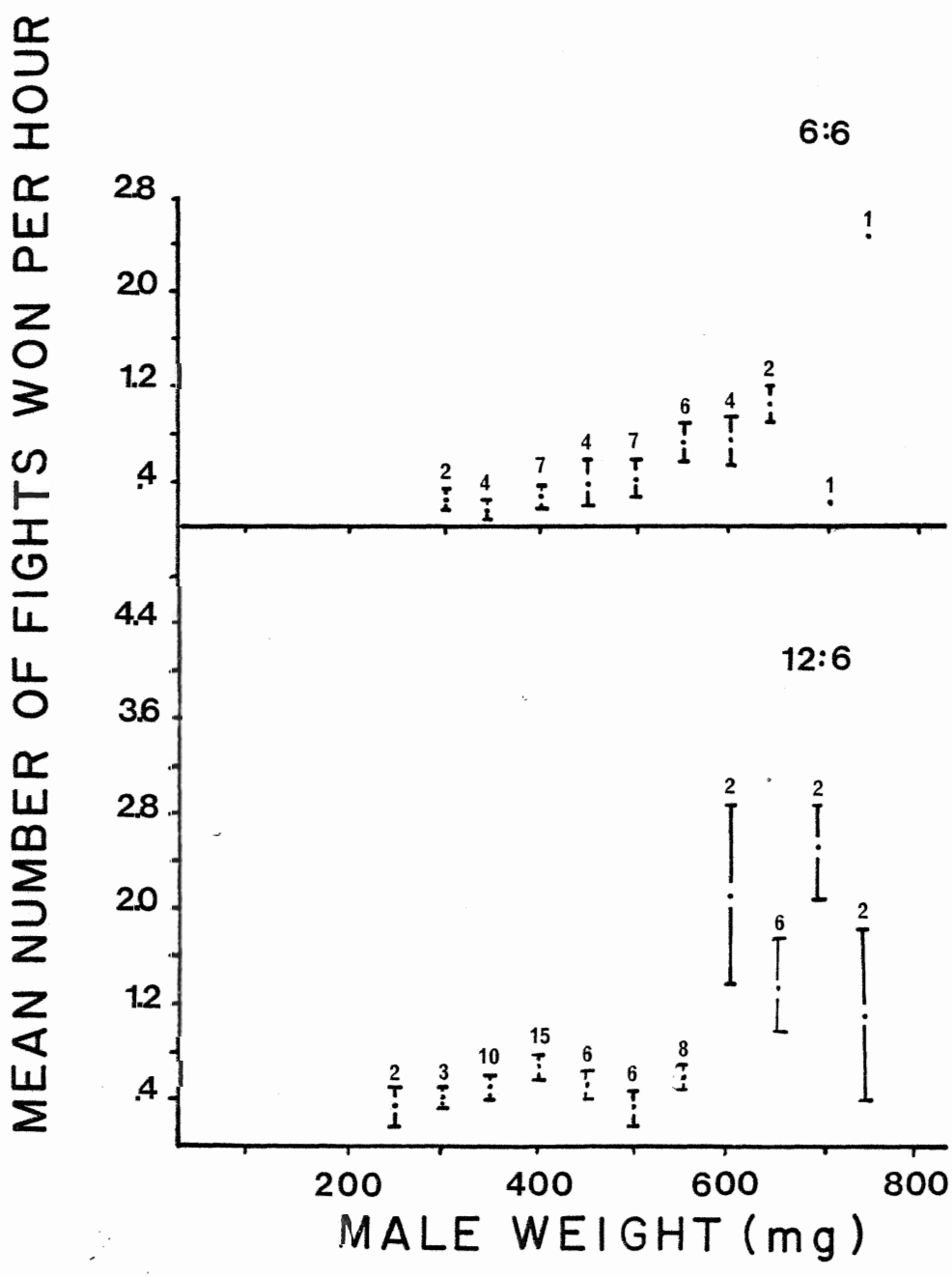

MEAN NUMBER OF FIGHTS WON PER HOUR
6:6
2.8
2.0
1.2
.4
12:6
4.4
3.6
2.8
2.0
1.2
.4
200
400
600
800
MALE WEIGHT (mg)

Figure 19

The mean percent of fights a male won (with standard errors) as a function of male weight at the low (six males and six females) and high (twelve males and six females) densities.

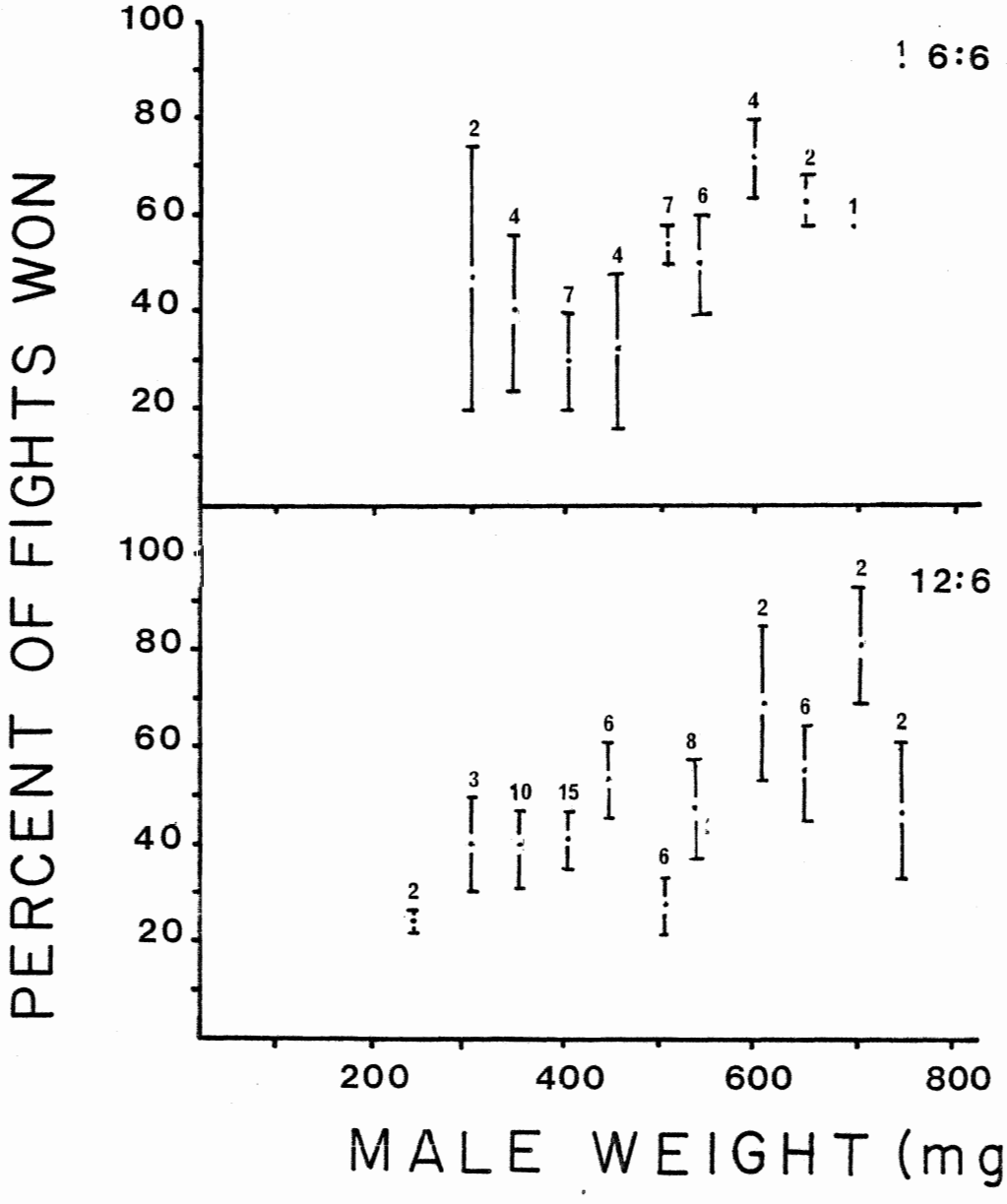
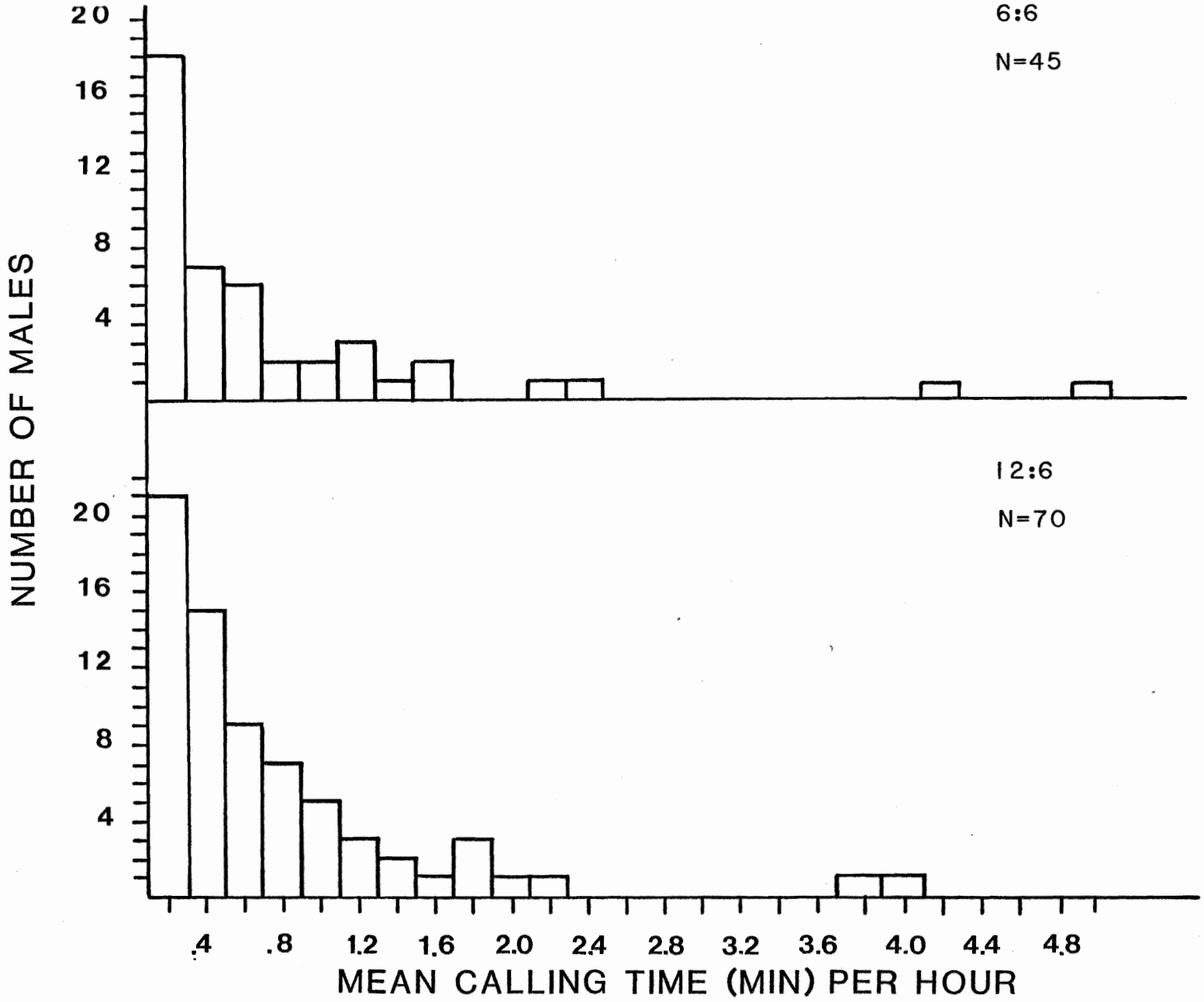

PERCENT OF FIGHTS WON
100
80
60
40
20
16:6
2
4
7
4
7
6
4
2
1
100
80
60
40
20
12:6
2
3
10
15
6
6
8
2
6
2
2
200
400
600
800
MALE WEIGHT (mg

Figure 20

Frequency distribution of the mean number of minutes individual males spent calling per hour at the low (six males and six females) and high (twelve males and six females) densities.


6:6
N=45
12:6
N=70
NUMBER OF MALES
20
16
12
8
4
.4
.8
1.2
1.6
2.0
2.4
2.8
3.2
3.6
4.0
4.4
4.8
MEAN CALLING TIME (MIN) PER HOUR

($\bar{X}$=0.69±0.15min) was not significantly different from that at the high density ($\bar{X}$=0.63±0.09min) (U-test,Z=0.582,p=0.28). Mean mating rates of males who called at different rates are in Fig. 21. Mean mating rates did not vary significantly with calling rates at the low (F=0.986,p=0.05) or high density (F=1.60, $p > 0.05$). The number of matings which were immediately preceded by calling are in Table 3. Matings not preceded by calling occurred significantly more often than those preceded by calling at the low density (χ^2=8.91,$p < 0.01$). However, there was no significant difference in the number of matings preceded or not preceded by calling at the high density (χ^2=1.45,$p > 0.05$).

Courting preceded all matings. The relationship between rates at which a) females were courted and b) males courted females, and male and female mating rates were examined at both densities. Frequency distributions of the rates at which females were courted by males are in Fig. 22. The mean time that females were courted at the low density ($\bar{X}$=0.855±0.83min) was significantly less than that at the high density ($\bar{X}$=1.18±0.118 min) (U-test,Z=2.28,p=0.011). Mating rates of females who were courted at different rates are in Fig. 23. Mean female mating rates did not vary significantly according to the time females were courted at the low (F=1.57,$p > 0.05$) or high density (F=1.00,$p > 0.05$). Frequency distributions of the rates at which males courted at both densities are in Fig. 24. The mean courting rates of males at the low ($\bar{X}$=0.86±0.14min) and high density ($\bar{X}$=0.713±0.07min) were not significantly different (U-test, Z=0.34,p=0.33). Mating rates of males who had different rates

Figure 21

The mean number of matings per hour (with standard errors) by males as a function of the mean number of minutes males spent calling per hour (with standard errors) at low (six males and six females) and high (twelve males and six females) densities. The small numbers above the standard error bars represent the number of males used to calculate the means.

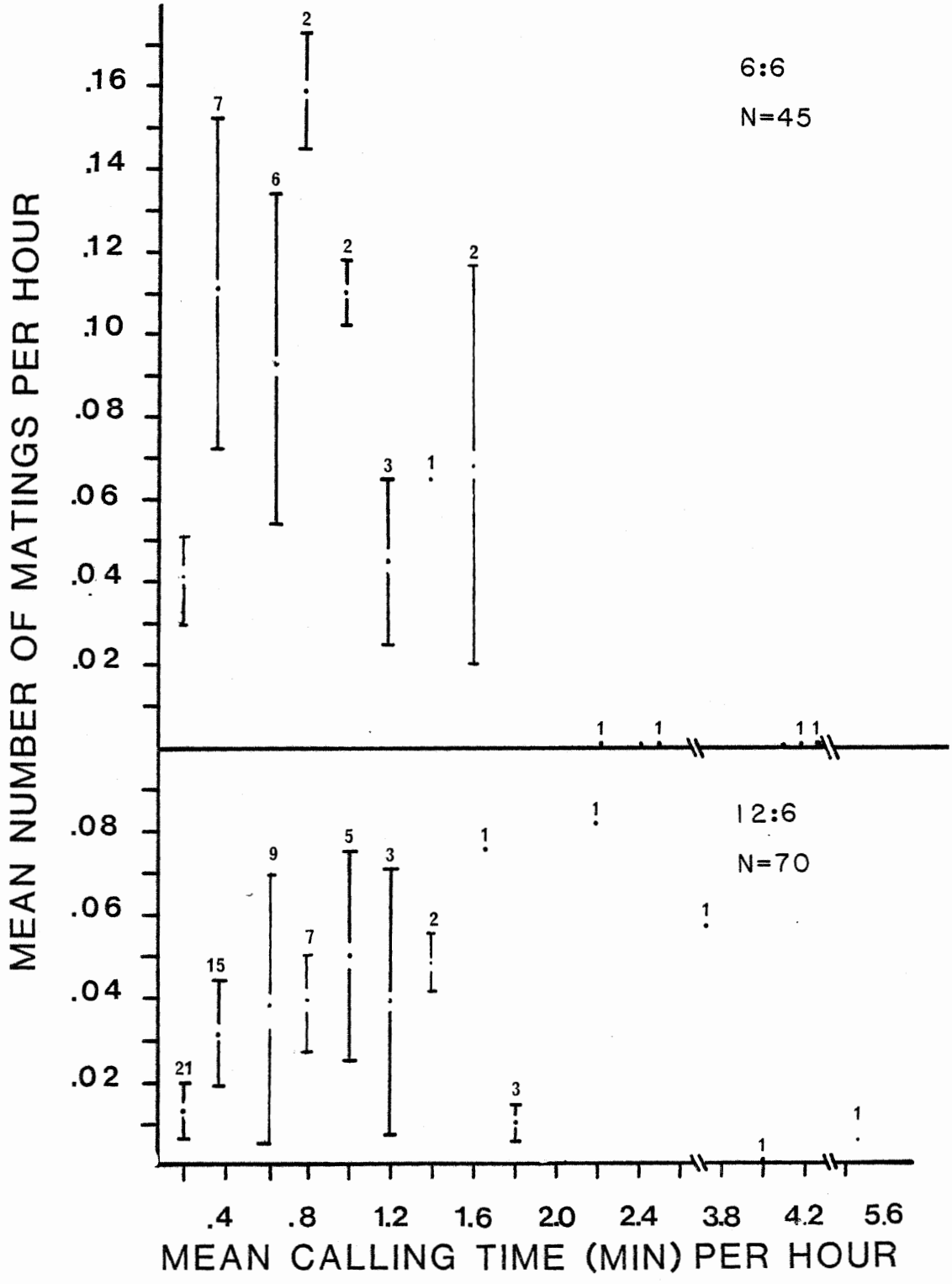

6:6
N=45
12:6
N=70
MEAN NUMBER OF MATINGS PER HOUR
.16
.14
.12
.10
.08
.06
.04
.02
.08
.06
.04
.02
.4
.8
1.2
1.6
2.0
2.4
3.8
4.2
5.6
MEAN CALLING TIME (MIN) PER HOUR

Table 3: The number of matings immediately preceded (within 30 min) by male calling at the low (six males and six females) and high (twelve males and six females) densities.

Density	Number of Matings Preceded by Calling Behaviours	Number of Matings Not Preceded by Calling Behaviours
Low	54	105
High	36	52
Total	90	157

Figure 22

Frequency distribution of the mean number of minutes individual females were courted per hour at low (six males and six females) and high (twelve males and six females) densities.

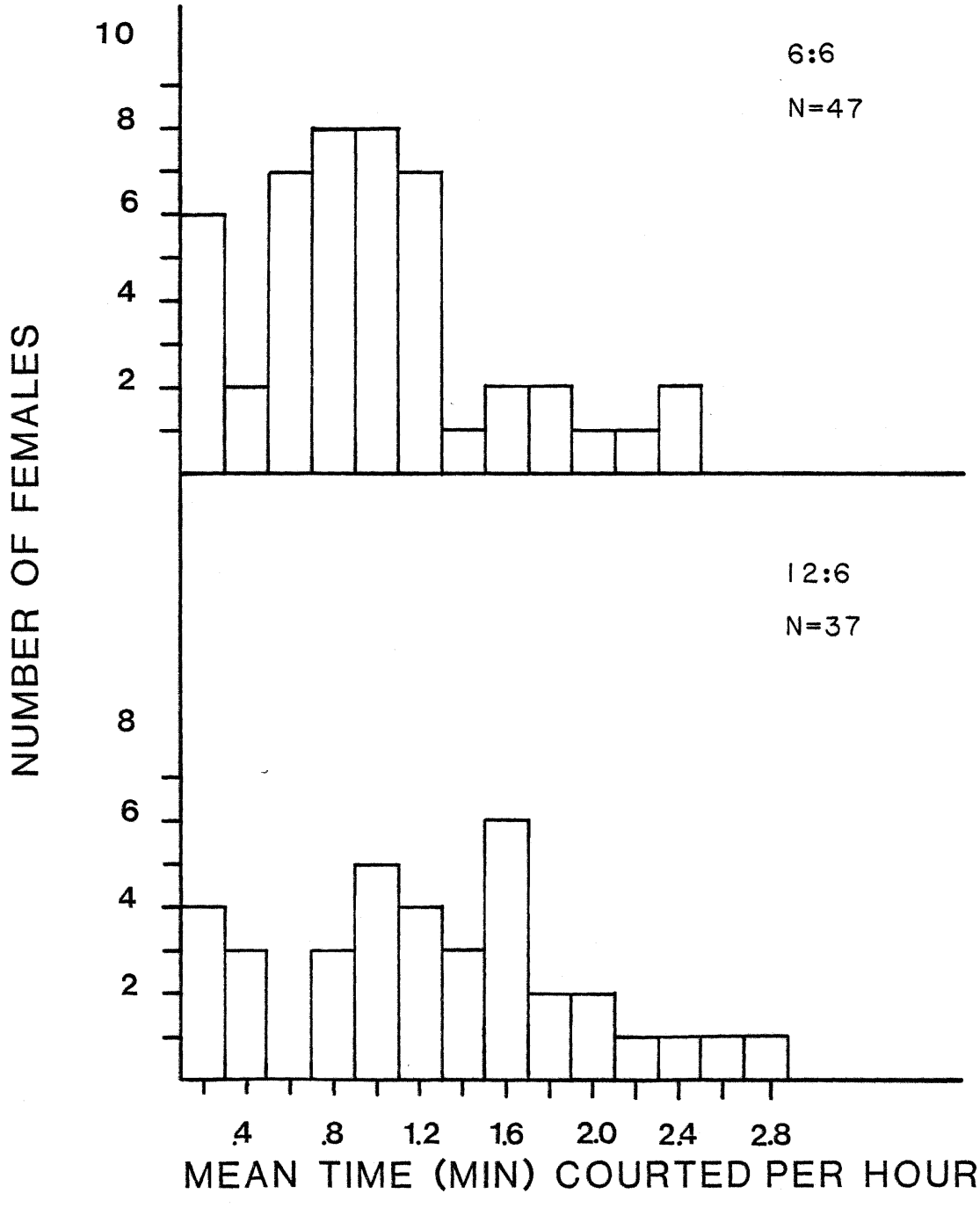

6:6
N=47
12:6
N=37
NUMBER OF FEMALES
10
8
6
4
2
8
6
4
2
.4
.8
1.2
1.6
2.0
2.4
2.8
MEAN TIME (MIN) COURTED PER HOUR

Figure 23

The mean number of matings per hour (with standard errors) by females as a function of the mean number of minutes females were courted per hour (with standard errors) at low (six males and six females) and high (twelve males and six females) densities. The small numbers above the standard error bars represent the number of females used to calculate the means.

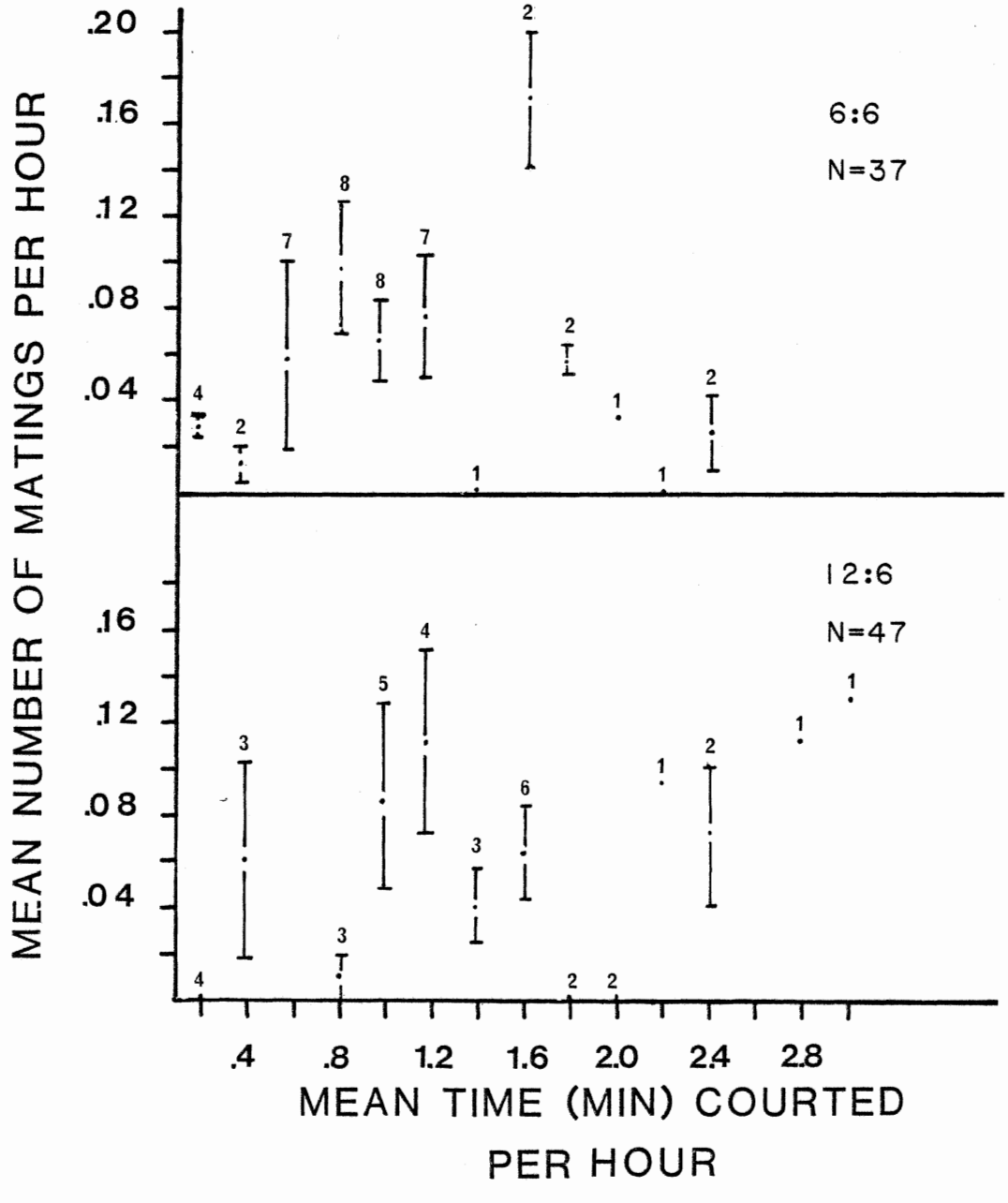
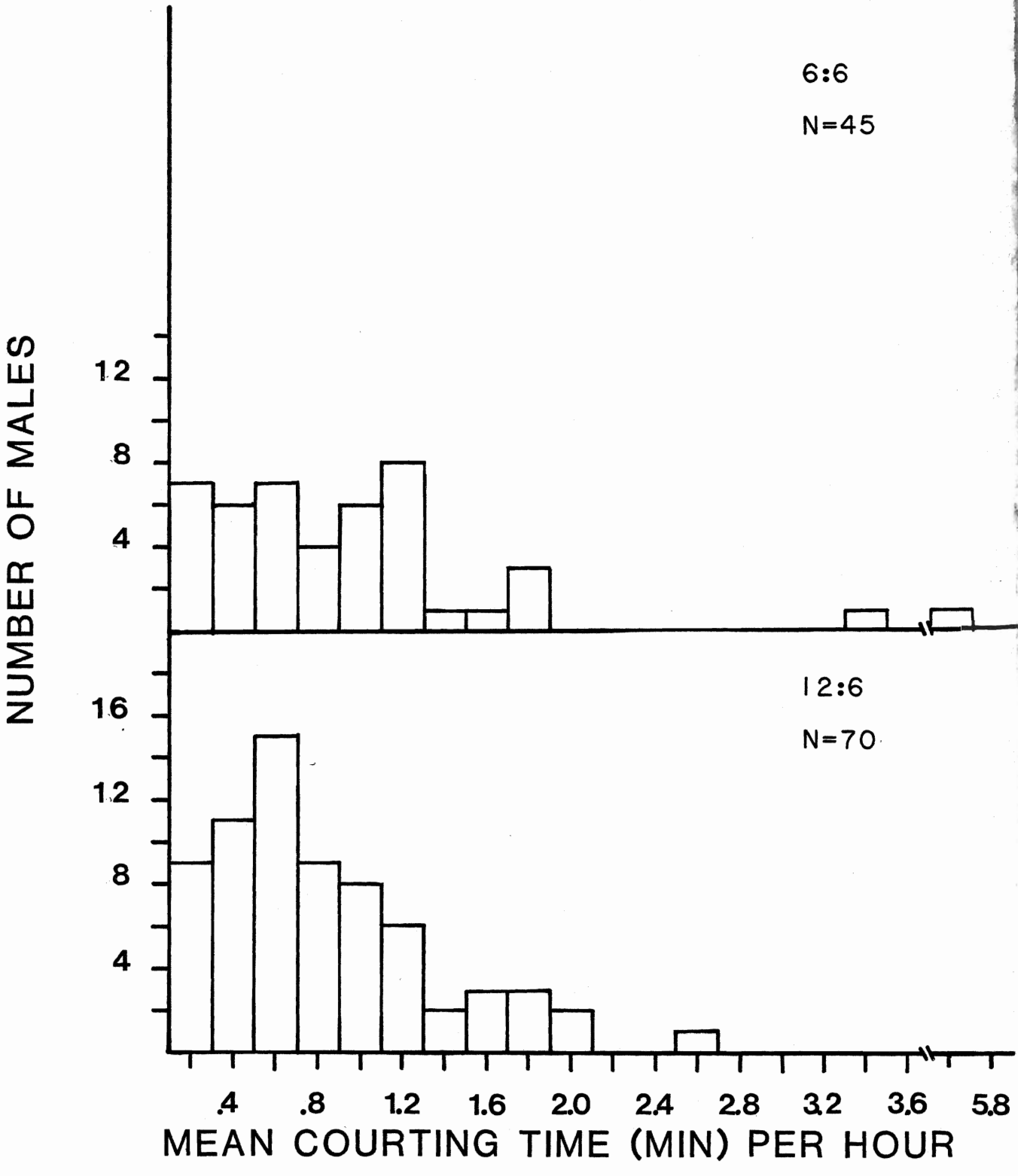

MEAN NUMBER OF MATINGS PER HOUR
.20
.16
.12
.08
.04
6:6
N=37
12:6
N=47
.4
.8
1.2
1.6
2.0
2.4
2.8
MEAN TIME (MIN) COURTED PER HOUR

Figure 24

Frequency distributions of the mean number of minutes males spent courting per hour (with standard errors) at the low (six males and six females) and high (twelve males and six females) densities.


6:6
N=45
12:6
N=70
NUMBER OF MALES
12
8
4
16
12
8
4
.4
.8
1.2
1.6
2.0
2.4
2.8
3.2
3.6
5.8
MEAN COURTING TIME (MIN) PER HOUR

of courtship are in Fig. 25. Mating rates varied significantly with the rates at which males courted in the low ($F=3.79, p < 0.05$) and high density ($F=1.99, p < 0.05$). A power fit was significant at the low density ($r=0.36, p < 0.05, Y=0.061(X)+0.02$), but there was no significant power fit for the high density data ($r=0.142$, $p > 0.05$, $Y=0.004(X)+0.027$). Lower and upper comparison limits for each mean are shown in Appendix Fig. 7. All intervals overlap, therefore no means are considered significantly different at the 0.05 experimentwise level of significance (Sokal and Rohlf 1969).

Post-copulatory Behaviour

In a successful mating a spermatophore is passed to the female and remains attached for sperm transfer. Females were known to remove the spermatophore by eating or rubbing them against the substrate (Table 4). Spermatophores were eaten by females significantly more often than they were rubbed off at the low ($\chi^2=11.88, p < 0.01$) and high density ($\chi^2=11.13, p < 0.01$). Females sometimes removed spermatophores during the post-copulatory guarding phase if the male was involved in a fight. More commonly, male courtship was associated with females removing attached spermatophores (Table 5). Of those observations in which the fate of the spermatophore was known, 67 percent of the females at the low density and 71.4 percent of those at the high density removed the spermatophore when first courted after mating.

Frequency distributions of the duration that spermatophores were retained are in Fig. 26. The mean duration that females

Figure 25

The mean number of matings per hour (with standard errors) by males as a function of the mean number of minutes males spent courting per hour (with standard errors) at the low (six males and six females) and high (twelve males and six females) densities.

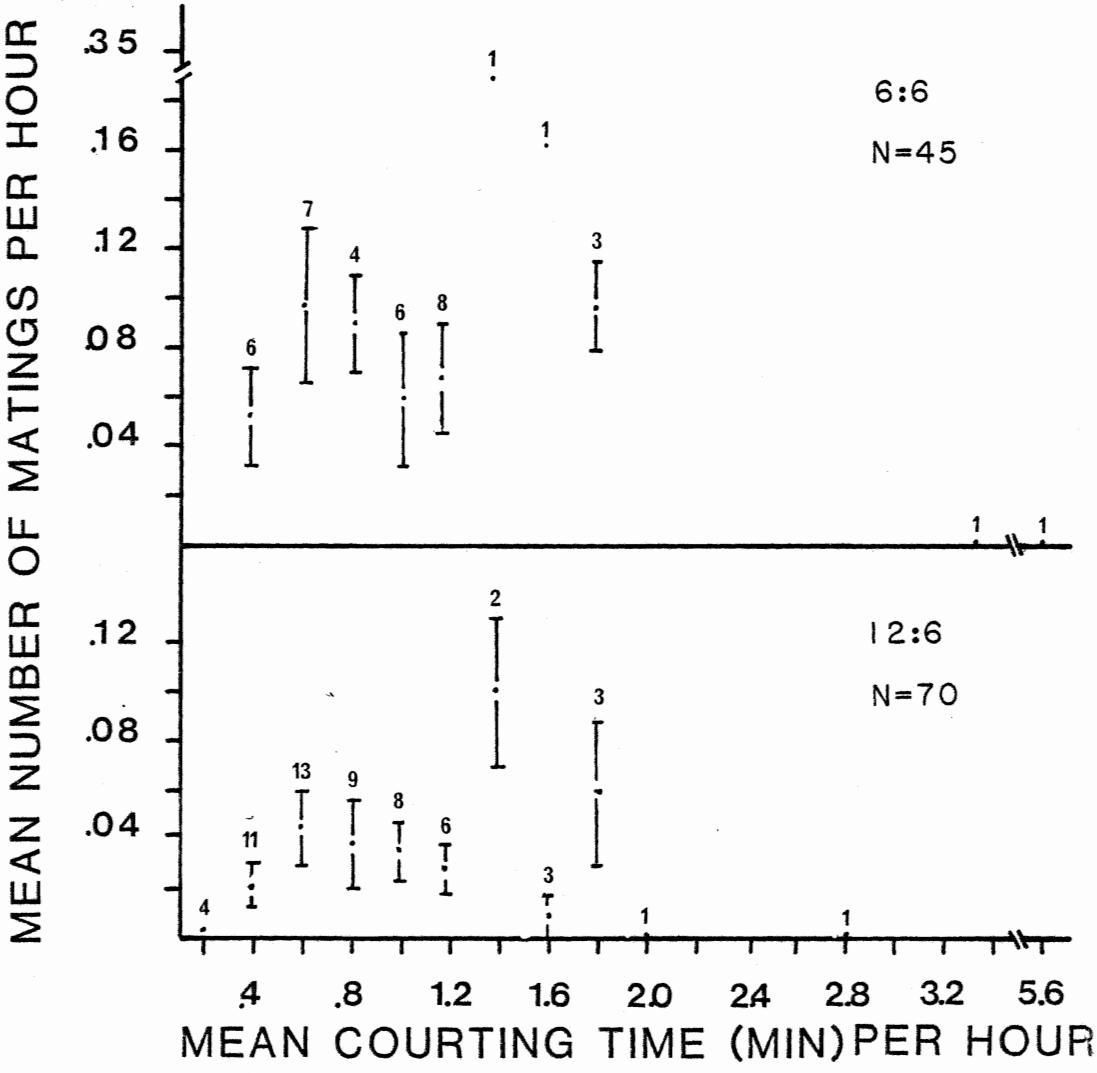

MEAN NUMBER OF MATINGS PER HOUR
.35
.16
.12
.08
.04
6:6
N=45
12:6
N=70
.4
.8
1.2
1.6
2.0
2.4
2.8
3.2
5.6
MEAN COURTING TIME (MIN) PER HOUR

Table 4: The number of spermatophores a) eaten b) rubbed off of c) of unknown fate at the low (six males and six females) and high (twelve males and six females) densities.

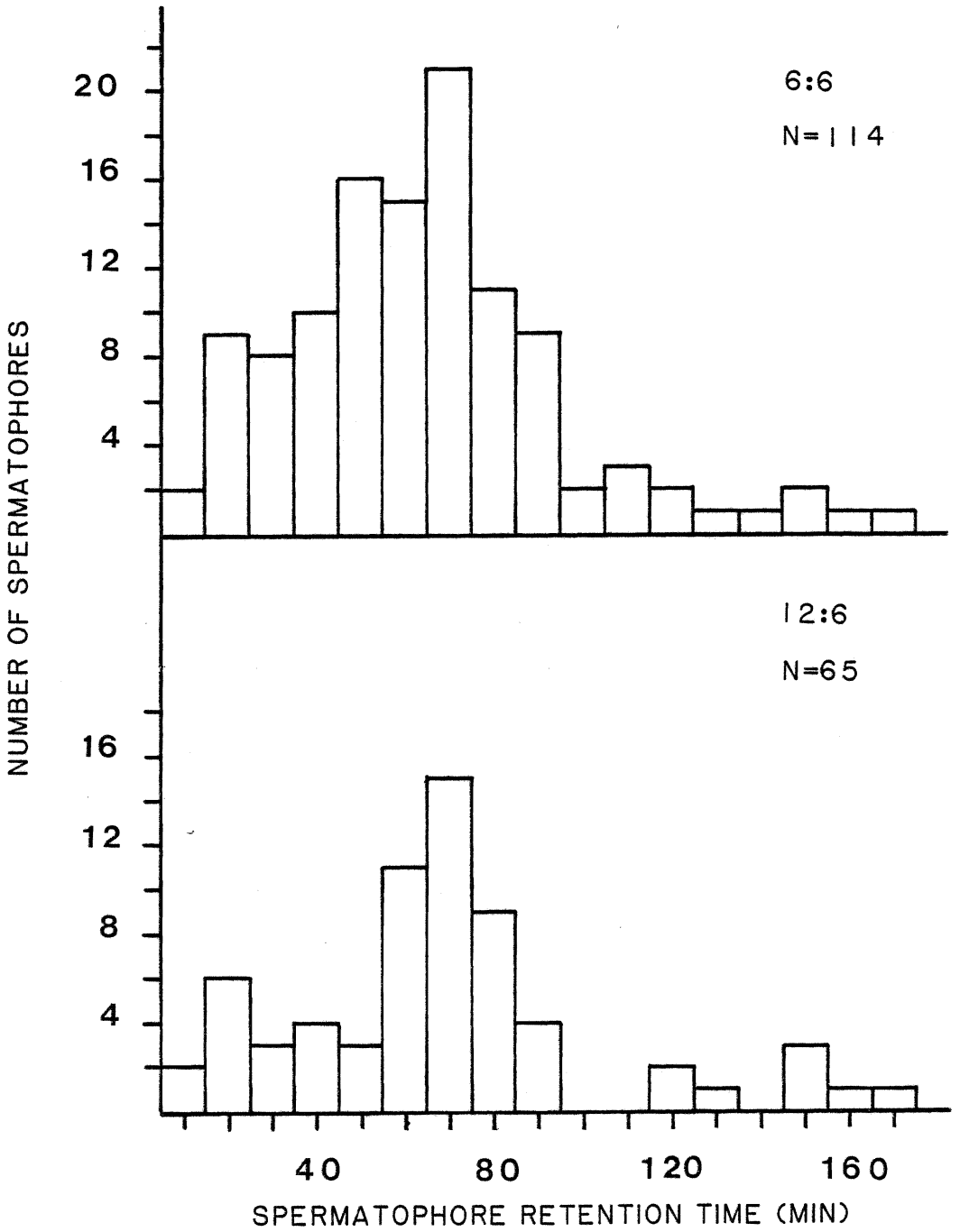
Density	Eaten	Rubbed Off	Unknown
Low	70	23	66
High	39	7	42
Total	109	30	108

Table 5: Spermatophore fates following the first bout of courtship after mating at low (six males and six females) and high (twelve males and six females) densities.

Density	Female Removes Spermatophore	Female Does Not Remove Spermatophore	Incomplete Information
Low	73	36	50
High	45	18	25
Total	118	54	75

Figure 26

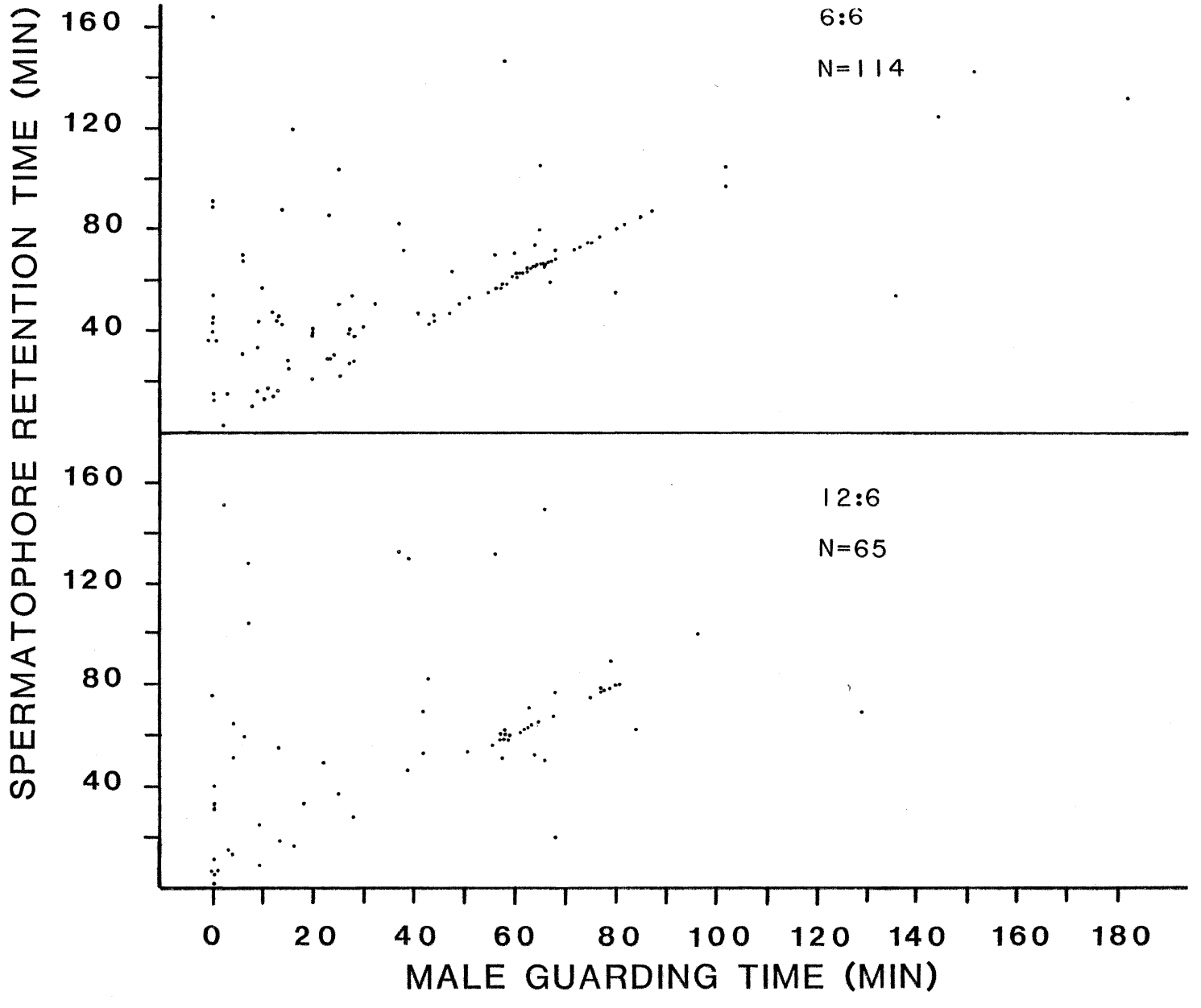
Frequency distributions of the time (min) spermatophores were retained by females at low (six males and six females) and high (twelve males and six females) densities.


6:6
N=114
12:6
N=65
NUMBER OF SPERMATOPHORES
20
16
12
8
4
16
12
8
4
40
80
120
160
SPERMATOPHORE RETENTION TIME (MIN)

retained spermatophores at the low density ($\bar{X}$=57.1±3.01min) was not significantly different from the high density ($\bar{X}$=62.1±4.11 min) (Z=0.751,p=0.227). In Fig. 27, spermatophore retention times are examined as a function of the duration that a male guarded the female after mating. Spermatophore retention times varied significantly according to the duration that a male guarded a female in both the low (F=2.29,$p < 0.05$) and high density (F=2.29,$p < 0.05$). Linear regressions were significant at both the low (r=0.665,$p < 0.01$,Y=0.534($\bar{X}$)+34.63) and high density (r=0.369,$p < 0.01$,Y=0.388(X)+46.27).

Figure 27

The duration a spermatophore was retained by a female (min) as a function of the time a male guarded (min) at the low (six males and six females) and high (twelve males and six females) densities.


SPERMATOPHORE RETENTION TIME (MIN)
160
120
80
40
6:6
N=114
160
120
80
40
12:6
N=65
0
20
40
60
80
100
120
140
160
180
MALE GUARDING TIME (MIN)

DISCUSSION

Rates of calling by male G. integer varied significantly over light and dark hours; by contrast, rates of courting and mating did not. Males called more frequently during the dark hours. Females are primarily phonotactic during the night hours (Cade 1979a); therefore, it is expected that male calling, used in mate attraction, should predominate during this period. Pressures acting on males and females to produce and respond to long range calls preferentially during the dark hours may relate to a reduction in the associated risks of predation (Bell 1979b, Walker 1964) and parasitism (Cade 1975). Courting does not provide highly directional long range cues (Alexander 1961). The regular production of the courtship song throughout the diel cycle incurs fewer costs than would calling. Cade (1979a) speculated that calling and intermittent signalling during daylight hours served to attract sexually active females at this time. Continuous rates of mating throughout the diel cycle in this study support the contention that females remain sexually active throughout the day. Diurnal calling and courting may effectively increase the number of mates procured. A baseline trial indicated females older than 18 days of age seldom mated. Females older than 18 days may be less receptive if their egg supply is exhausted or if they have senesced. Female mating rates did not vary significantly with age up to 18 days. Newly molted A. domesticus females avoid male calls at one day of age and seldom mate (Popov and Shuvalov 1977). In this study newly eclosed females could not avoid males because of the arena design and mated at rates similar to older females.

Mating rates of sexually mature male G. integer did not vary significantly with age. G. integer are a short-lived species, with determinate growth, and reproductive opportunities limited to one season. Therefore, they are expected to exert maximum reproductive effort throughout their lives. This contrasts with patterns of reproductive effort by long-lived species where size and experience may increase through time and influence breeding opportunities (Howard 1978, Pugesek 1981). In such species, mating activity may increase with male age since the residual reproductive value of older males is reduced and increases in lifetime fitness derived from increased reproductive effort will surpass benefits of a lengthened lifespan (Williams 1966).

Bradbury (1981) proposed that males within clusters mate more on average than isolated males in lek species if females prefer males in aggregations. In the field, male G. integer call in loose aggregations similar to vertebrate leks (Cade 1981b). The six and twelve male densities used in these experiments represent natural population densities (Cade pers. comm.). Increments in the mean male mating rates at higher densities may be the result of two factors; females present in leks may mate more frequently because of some form of social stimulation; or males in dense clusters may attract greater numbers of females. The data presented here address the first hypothesis. That is, do females mate more frequently when more males are available? Female mating rates were not significantly different, however, between densities. Similar percentages of females never mated during observations. Females do not mate more often simply because of

increased social stimulation. Increases in male mating rates at high densities may be due to increases in the number of females attracted to aggregations, not increases in the number of matings by those females present. Bradbury (1981) argued that aggregated males do not attract more females on a per male basis because of increases in the time or range that signals are transmitted, but because females prefer aggregations. In this study the mean mating rates of males in the low density were significantly greater than those of high density males. The ratio of mated to non-mated males did not vary significantly between densities. Differences in male mating rates between densities may be due to the sex ratio differences between densities. At low male densities, there are fewer competitors for the same number of potential mates. Males at low densities may realize greater rates of mating because mates are more monopolizable than at the high density (Emlen and Oring 1977). Mating rates of males at the high density were doubled to approximate rates at the high density when the sex ratio is equal. This adjustment indicated there were no significant differences in male mating rates between densities. This suggests that increases in the number of females attracted to leks lead to greater male success. Cade (1981b) used loudspeakers broadcasting male G. integer calling song to examine the number of females attracted to isolated and clumped loudspeakers. He found no significant difference between densities in the number of females attracted, per loudspeaker, in contrast to Bradbury's hypothesis. Further

experimentation using live males in dense and sparse aggregations, and measurement of the duration that females remain in each situation, may clarify the discrepancy between findings of Cade and the expectations of Bradbury and corresponding results of this study.

Males and females in this study mated with as many as three different partners in a day. Remating by female G. integer can reduce the probability of reproductive failure when spermatozoa or egg development stimulants are not successfully transferred (Sakuluk and Cade 1980). Furthermore, females mating with different males may have more heterogenous offspring, possibly capable of withstanding a greater variety of environmental conditions (West-Eberhard 1979). Females may also acquire nutrition by consuming spermatophores received in mating (Sakuluk and Cade 1980). Multiple matings by a male increase the chances of his spermatozoa successfully fertilizing a female's eggs because of the successful transfer of spermatozoa or egg development stimulants (Sakuluk and Cade 1980) or precedence of his sperm over that of other males (Parker 1970b).

Bateman (1948) demonstrated that male reproductive success is more variable than female reproductive success in Drosophila melanogaster. Mating rates can be viewed as an indirect measure of reproductive success. Variances in male and female mating rates are homogeneous at the low density but heterogenous at the high density, with the variance in male mating rates less than female variance. In this species, mating rates may not be a good estimate of reproductive success since the number of

spermatophores passed to the female is not proportional to the number of eggs fertilized (see Sakuluk and Cade 1981).

The variances of both male and female mating rates at the low density were significantly greater than high density variances. Reasons for the greater variance in low density female mating rates are obscure. The greater variance in male mating rates at the low compared to high density may be a result of an increased ability of males at low density to defend and mate with females. Reduced defensibility of females at high densities may reduce the variance in male mating rates.

Alexander (1961) predicted that male crickets at low densities will be more territorial than males at high densities. Male tendencies toward territoriality in field situations may result in reduced locomotion in the lab. Rates of male movement at both densities considered here were not significantly different, contrary to Alexander's predictions. Male territoriality may not have been accurately assessed by rates of movement. Rates of movement by females were significantly greater than those of males at both densities. Increased locomotory habits of females are often found in insects since a female can colonize an area once she is fertilized (Alexander 1961). It is also expected that female G. integer will move more than males since they must orient to male calling song to mate. Rates of female movement did not differ between densities and did not vary significantly with mating rates at either density. Reproductive benefits associated with female movement may reside in the ability of females

to locate calling males from greater distances than those in the lab.

Alexander (1961) suggested that male crickets will adopt silent searching behaviours to acquire mates, more often than fight, at high relative to low densities. Such density-related shifts in behaviour will result in increased male mating success and suggest that reproductive payoffs associated with competition are reduced at high densities. In this study, male mating rates varied significantly with fighting rates at the low but not high density. The significant power fit between mating and fighting rates at the low density indicates that this form of mating effort was profitable, but at relatively high levels yielded diminishing returns.

In this study, increased numbers of males at the high density increased the likelihood of encounters and subsequent fights. Indeed, the mean rate of male fighting at the high density was significantly greater than that at the low density. The fighting rates by males at the low density were doubled to adjust for the presence of twice as many males in the high density. Doubled rates of male fighting at the low density were significantly greater than at the high density, suggesting fighting tendencies of males at low densities are greater than those of males at high densities. Alexander (1961) stated that males at low densities have greater fighting tendencies than males at high densities. Fighting requires time and energy and may reduce an individual's lifespan. Increased rates of fighting by low density males may result from the ability of such males to defend

a territory or mate economically. The net reproductive benefits of alternate forms of mating effort, such as searching, may be greater than those of fighting at high densities. Rates of movement were used to approximate the extent of searching. Male mating rates did not vary significantly with movement rates. In the field, satellite male G. integer patrol the area around calling males for females (Cade 1975). Rates of movement used in my study may not be representative of short distances used in searching.

Females capable of mate choice are expected to mate with dominant males hence gain either genetic or resource benefits (Trivers 1972). Females may prefer males in dense aggregations over more uniformly distributed males if direct comparisons of male phenotype are facilitated and mate choice by other females more easily monitored (Bradbury 1981). In this study, three criteria were used to measure male dominance. In matings immediately preceded by fights, victors mated significantly more often than losers. However, over 50 percent of the matings were not preceded by a fight. Male field crickets form relatively stable linear hierarchies (Alexander 1961), and this may reduce the number of fights prior to mating. The possibility that established male dominance may influence female mating decisions was examined. Bradbury (1981) predicted that low ranking males at high densities will have marginally better expectations of lifetime fitness than such males at low densities. Male mating rates did not vary significantly with rates of winning. Rates of winning in part depend upon the number of fights in which a male

was involved. Although the total number of fights by individual males decreases gradually towards the bottom of the hierarchy (Alexander 1961), the frequency at which males fight may obscure the relationship between winning and dominance status. Hence, mating rates were examined as a function of the percentage of fights an individual won, independent of the frequency at which he fought. There was a significant power fit between mating rates and the percentage of fights an individual won at low density. This indicates that the percentage of fights an individual won resulted in increased mating success until mating rate gains were below the level of profitability.

Females at the low density mated with dominant males to a greater extent than those at the high density. This may be due to a preference of females to mate with dominant males, or the ability of dominant males to monopolize female mating opportunities. At the high density, mating rates did not vary significantly with the percentage of fights a male won. Dominant males at high densities may obtain fewer mating benefits than males at low densities because of increased costs of resource defensibility. Furthermore, at high densities, the probability of male-male interactions is higher and there is a premium on males mating without interference from other males. Low ranking males may utilize alternate (silent) satellite strategies. By using less conspicuous behaviours than high ranking males, they may be interrupted less during courtship.

Male dominance status may increase the male's ability to monopolize females and/or be preferred by females. Male success

in fights preceding matings may have increased his mating success for either of the above stated reasons. The two different male densities used in these experiments provided an empirical measure of the degree of monopolizability of mates (Emlen and Oring 1977). The ability of males to monopolize females is reduced at high densities. Females did not exert a consistent, density-independent, preference to mate with dominant males (as measured by their longterm success in fighting). The ability of males to monopolize resources, through male-male competition, may be a more powerful force influencing male mating success than the preference of females for specific males.

Male weight was significantly related to mating and fighting rates at the low but not high density. There was a significant linear relationship between male mating rates and weight at the low density. Heavier males, at the low density, may be more likely to fight because they are better able to defend resources and subsequently mate more than males at high densities. Rates at which males won fights were significantly related to weight at both densities. Alexander (1961) reported that male weight may influence dominance status. However, my data do not conclusively support this since the percent of fights an individual won did not vary with male weight at either density. In this study, calling rates were not significantly different between densities. Alexander (1961) stated that male crickets will call more at low densities than at high densities. Increased durations of male calling at the low density increase the chances of attracting females. The data do not support Alexander's

contention but calling rates in laboratory arenas are reduced when females are present (Wyatt 1982). The presence of females in the arenas may have reduced calling to minimal levels, such that density effects were not observed. Wyatt (1982) has shown that male G. integer call more in low density enclosed outdoor populations than under high density conditions. Since calling entails substantial costs in terms of the attraction of predators, parasites or other competing males (Cade 1975), it is to the male's advantage to reduce calling to a minimum once females are present.

Calling behaviour assures a female G. integer that a male is of the same species, the opposite sex, and may also be correlated with higher male fitness and/or the possession of suitable oviposition sites (Cade 1979a). Female house crickets, A. domesticus, can apparently distinguish dominant and subordinate male calling songs (Crankshaw 1979). Females responding preferentially to a loud enduring singer can quickly locate the male and obtain a successful mating. It was predicted, therefore, that female G. integer prefer calling males (Cade 1979a). In this study, females did not require males to call prior to mating. Furthermore, male mating rates did not vary significantly with their rates of calling. The readiness of females to mate with males who called little may indicate that noncalling males are more successful reproductively in field populations than was proposed by Cade (1979a). Females did not appear to select males based on the production of the calling song in the species studied here.

The consistent production of courtship song prior to all matings in this study suggests that at least short bouts of courtship are essential to mating. Courtship song may provide the female with information regarding male quality (Thornhill 1979). Courtship advertises male readiness to mate and stimulates females to mount in the crickets A. domesticus (Crankshaw 1979) and T. oceanicus (Burk 1979). Although Crankshaw (1979) suggested that courtship song may serve as a species specific identification signal, it is not likely to be important in species isolation since courtship songs are similar for many species (Alexander 1962). In females capable of mate choice, the time spent in courtship may improve the female's choice of mates. Long bouts of courtship allow the female to test males for genetically based characteristics that might contribute to the fitness of offspring and may facilitate mate choice if other males are attracted and compared (Thornhill 1979, Kirkendall unpub. ms). Rates at which females were courted at the low density were significantly less than rates at the high density. However, female mating rates did not vary significantly with the rates that they were courted. If a threshold level of courtship to ensure mating success exists, it has been exceeded. All female G. integer apparently require a minimum bout of courtship song prior to mating; however, they do not mate more often when they receive greater rates of courtship.

Rates of courtship did not differ significantly between densities, suggesting this form of male mating effort is not reduced at high densities. Male mating rates varied significantly with the rates that they courted at both densities but a

significant power fit was found only at the low density. Such a fit indicates that increased rates of male courtship by males at low density resulted in increased mating benefits; however, at high levels, courtship became ineffectual and did not further increase mating rates. There was no significant linear, exponential or power fit between rates of mating and courting at the high density although these components varied significantly. An unplanned comparison of means indicated no significant differences in male mating rates at different courtship intervals, using the 0.05 experimentwise level of significance (Sokal and Rohlf 1969). The significant ANOVA at the high density may have been due to a Type 1 error (i.e. rejection of a true null hypothesis). Additionally, it is more difficult to obtain levels of significance with an experimentwise test. Increased rates of courtship by males at high densities did not lead to mating rate increases. The probability that males at high density will be interrupted during courtship is increased. The lack of a significant relationship may be due to reduced resource defensibility because of interruption.

In this study a significant positive linear relationship between male guarding times and the duration that a spermatophore was retained existed at both densities. Male guarding in G. integer often involves inter-male aggression, prevents other males from courting and prevents the female from removing the spermatophore (Alexander 1961). Females commonly consumed the spermatophore. By doing so, females acquire nutrition (Sakuluk and Cade 1980) and may limit the extent to which they are

fertilized. In this study, courtship by the guarding male or another male stimulated spermatophore removal. The duration that a spermatophore is retained correlates positively with the degree of insemination in field crickets (Sakuluk and Cade 1981). Male guarding may ensure the male that all of his sperm have been transmitted. It may also increase the probability that the guarding male's sperm will fertilize the female's eggs through sperm competition or precedence (Parker 1970b). The mean spermatophore retention times of 57 and 62 min at low and high densities did not differ significantly. Males at both densities may be able to exert effective control over female mating decisions by repelling other males throughout this period. Alternatively, females may be choosing to remain with males for this period of time. By doing so they may avoid potentially detrimental courtship from other males (Daly 1978).

Conclusions

In crickets, male-male competition is an important parameter affecting male mating success. Dominant males may be chosen by females or better able to defend and mate with females. There is no conclusive evidence that females prefer to mate with dominant males. In these experiments, males and females were confined to indoor steel arenas. This experimental design may have altered acoustical conditions. Furthermore, it did not allow individuals to immigrate or emigrate. Doubling of mating and fighting rates to adjust for sex ratio differences between densities assumed that these behaviours increased linearly with density. Results from indoor arenas therefore may not reflect those from natural populations.

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Appendix Table 1

The initiation and termination dates for replicate trials of crickets, G. integer, at low (six males and six females) and high (twelve males and six females) densities.

Density	Replicate Run	Initiation (1980) Date	Initiation (1980) Month	Termination (1980) Date	Termination (1980) Month	Number of Days Observed
Low	1	10	April	28	April	14
	2	5	May	19	April	6
	3	13	June	2	July	14
	4	28	July	28	July	11
	5	13	July	13	August	7
High	1	4	May	17	May	6
	2	22	June	7	June	12
	3	4	July	21	June	13
	4	30	July	14	August	7

Appendix Table 2

The range and mean ages (with standard deviations) of female and male crickets (Gryllus integer) at the time of introduction in replicate trials at the low (six males and six females) and high (twelve males and six females) densities.

		Males				Females			
Density	Run	Range	n	Mean Age	Standard Deviation	Range	n	Mean Age	Standard Deviation
Low	1	4-41	10	16.5	3.30	1-14	14	5.5	1.97
	2	4-40	8	12.88	2.84	0-4	6	1.3	1.17
	3	4-46	11	19.09	3.14	0-5	13	2.15	1.29
	4	4-30	6	6.93	2.14	1-3	7	2.43	0.86
	5	5-28	9	10	2.29	0-2	10	13	0.88
High	1	4-38	18	15.44	2.72	1-3	9	2.0	0.91
	2	5-46	13	9.85	2.54	0-7	10	2.8	1.42
	3	5-36	12	13.75	3.50	1-4	11	1.73	0.93
	4	4.37	18	10.67	2.58	0-19	9	4.0	2.36

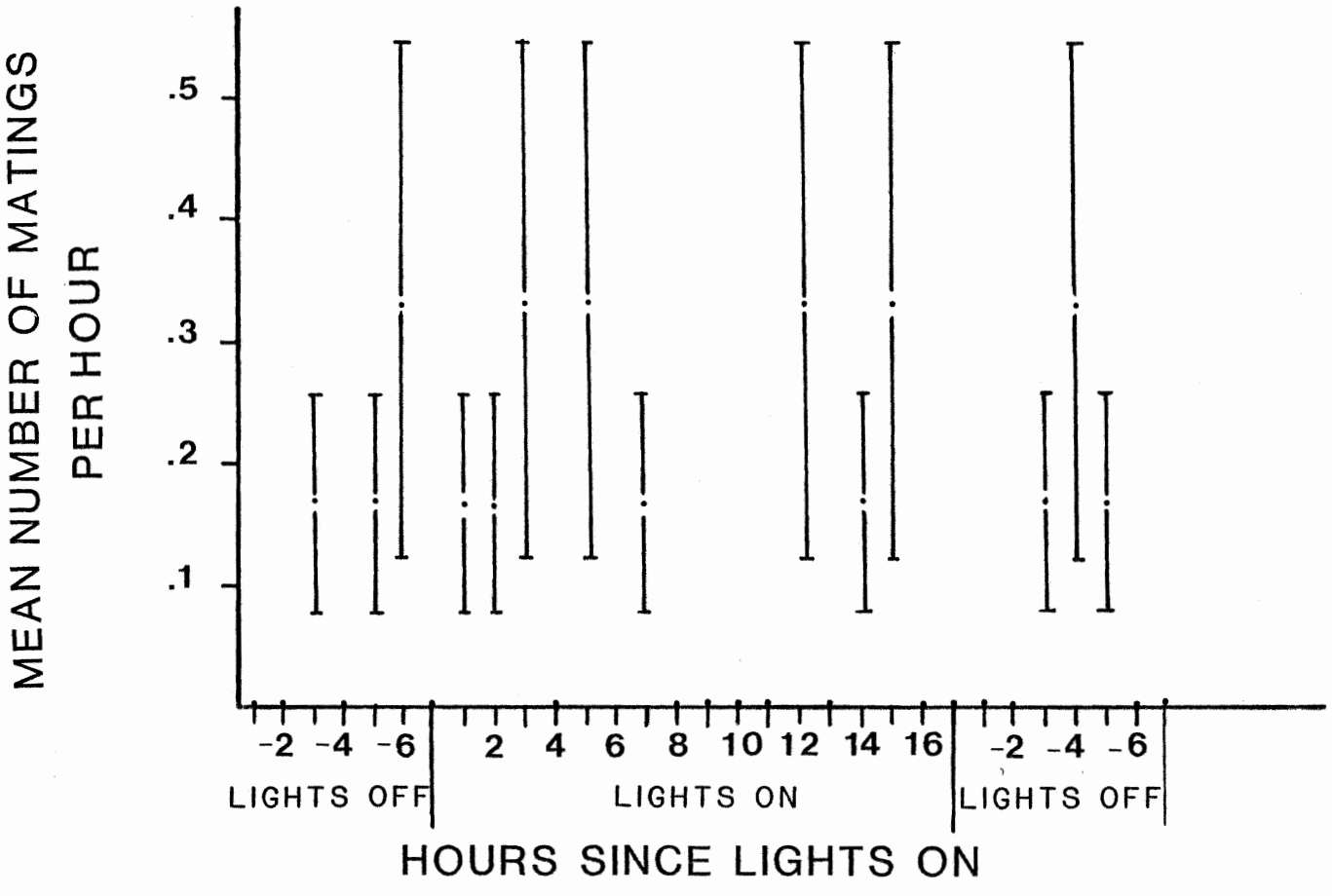
Appendix Table 3

Number of times females mated at different ages as determined by 30 days of observations in a high density population (twelve males and six females). Observations were conducted on consecutive days (except for eight instances, days 3, 4, 9, 14, 16, 21, 23, 27) following trial initiation.

Age	Number Females Observed	Number Matings	Age	Number Females Observed	Number Matings
1	6	0	17	5	0
2	6	0	18	3	0
3	7	0	19	4	0
4	9	0	20	1	0
5	7	2	21	5	1
6	6	2	22	2	0
7	5	0	23	4	0
8	6	1	24	4	0
9	5	2	25	2	0
10	6	6	26	2	1
11	7	0	27	2	0
12	2	6	28	0	0
13	7	0	29	2	0
14	3	5	30	0	0
15	4	1	31	0	0
16	4	2	32	2	0

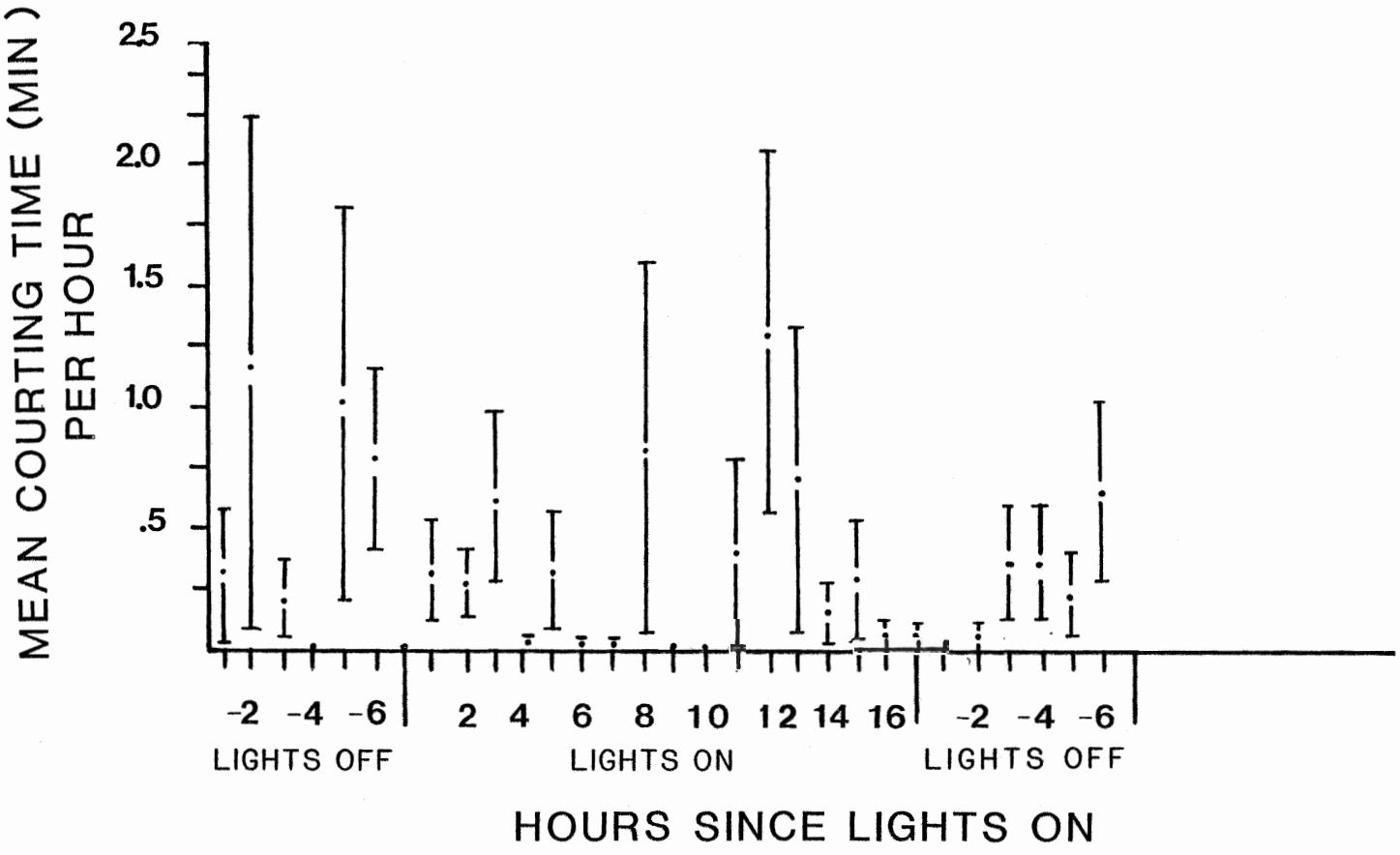
Appendix Figure 1

The mean number of matings per hour by six males observed continuously over a 30 h period throughout 13 hours of dark and 17 hours of light in a 17L:7D diel cycle.


MEAN NUMBER OF MATINGS PER HOUR
.5
.4
.3
.2
.1
-2 -4 -6
2 4 6 8 10 12 14 16
-2 -4 -6
LIGHTS OFF
LIGHTS ON
LIGHTS OFF
HOURS SINCE LIGHTS ON

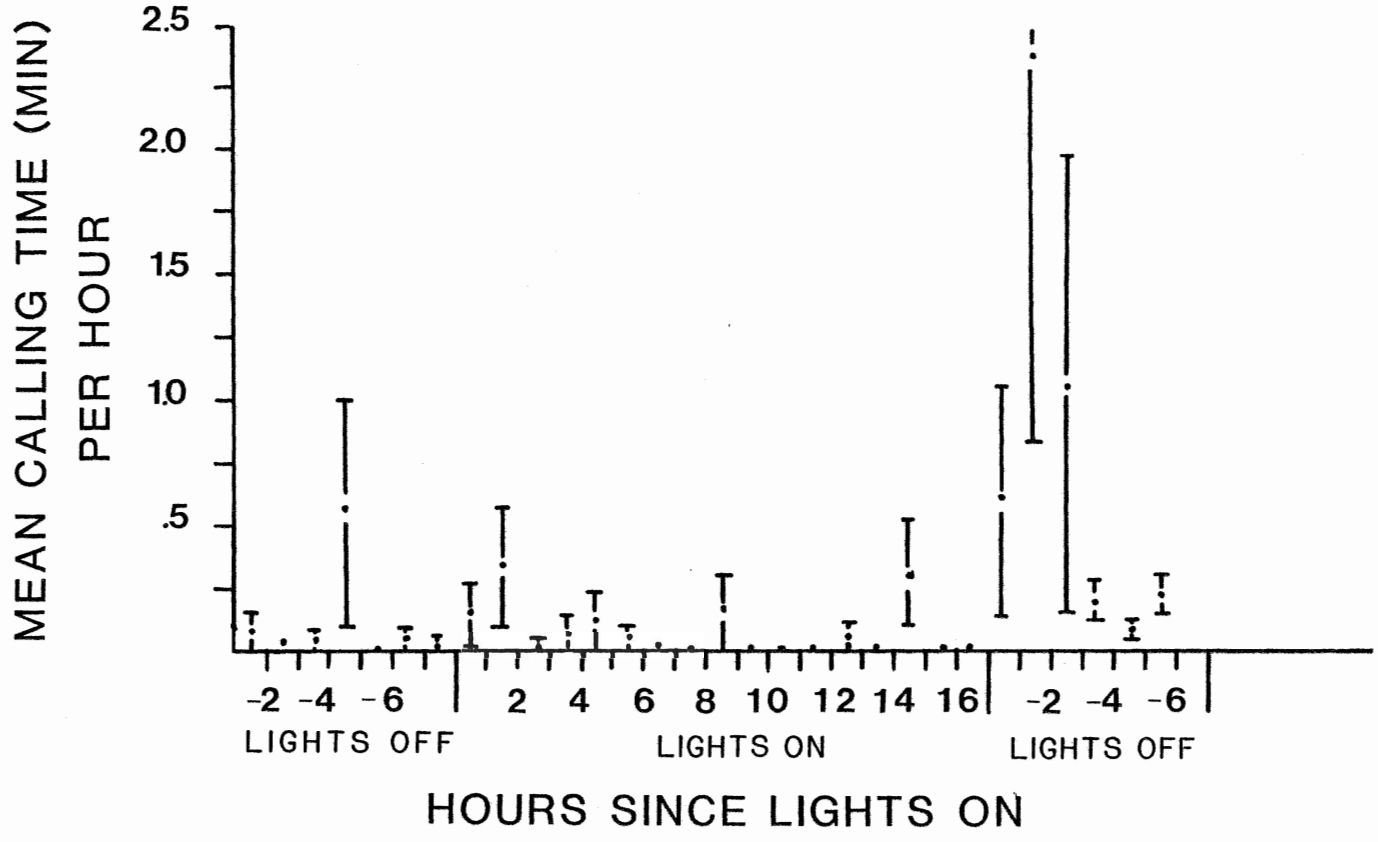
Appendix Figure 2

The mean number of minutes spent courting per hour by six males observed continuously for 30 hours throughout 13 hours of dark and 17 hours of light in a 17L:7D diel cycle.


MEAN COURTING TIME (MIN) PER HOUR
2.5
2.0
1.5
1.0
.5
-2 -4 -6
2 4 6 8 10 12 14 16
-2 -4 -6
LIGHTS OFF
LIGHTS ON
LIGHTS OFF
HOURS SINCE LIGHTS ON

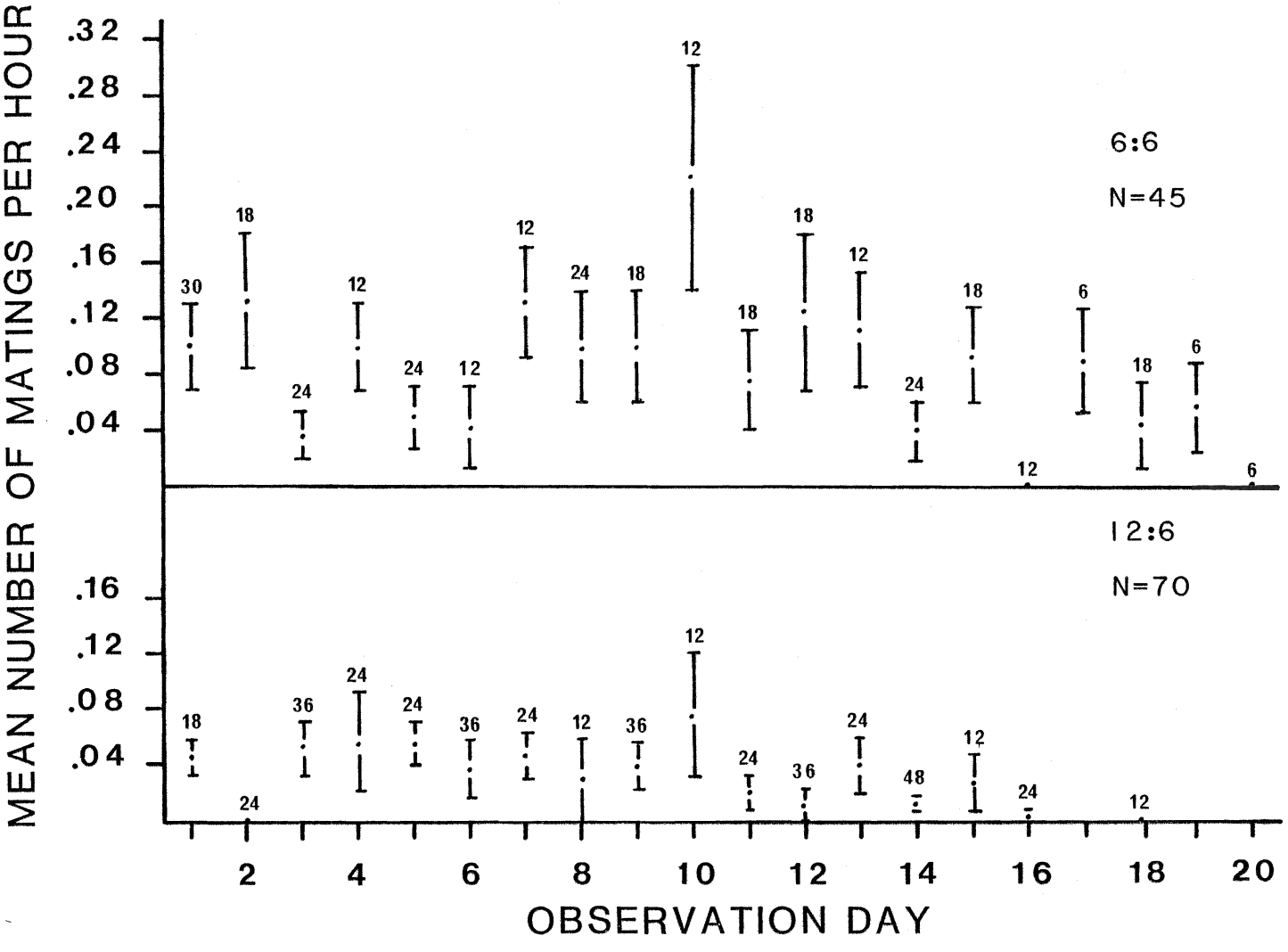
Appendix Figure 3

The mean number of minutes spent calling per hour by six males observed continuously for 30 hours throughout 13 hours of dark and 17 hours of light in a 17L:7D diel cycle.


MEAN CALLING TIME (MIN)
PER HOUR
2.5
2.0
1.5
1.0
.5
-2 -4 -6
2 4 6 8 10 12 14 16
-2 -4 -6
LIGHTS OFF
LIGHTS ON
LIGHTS OFF
HOURS SINCE LIGHTS ON

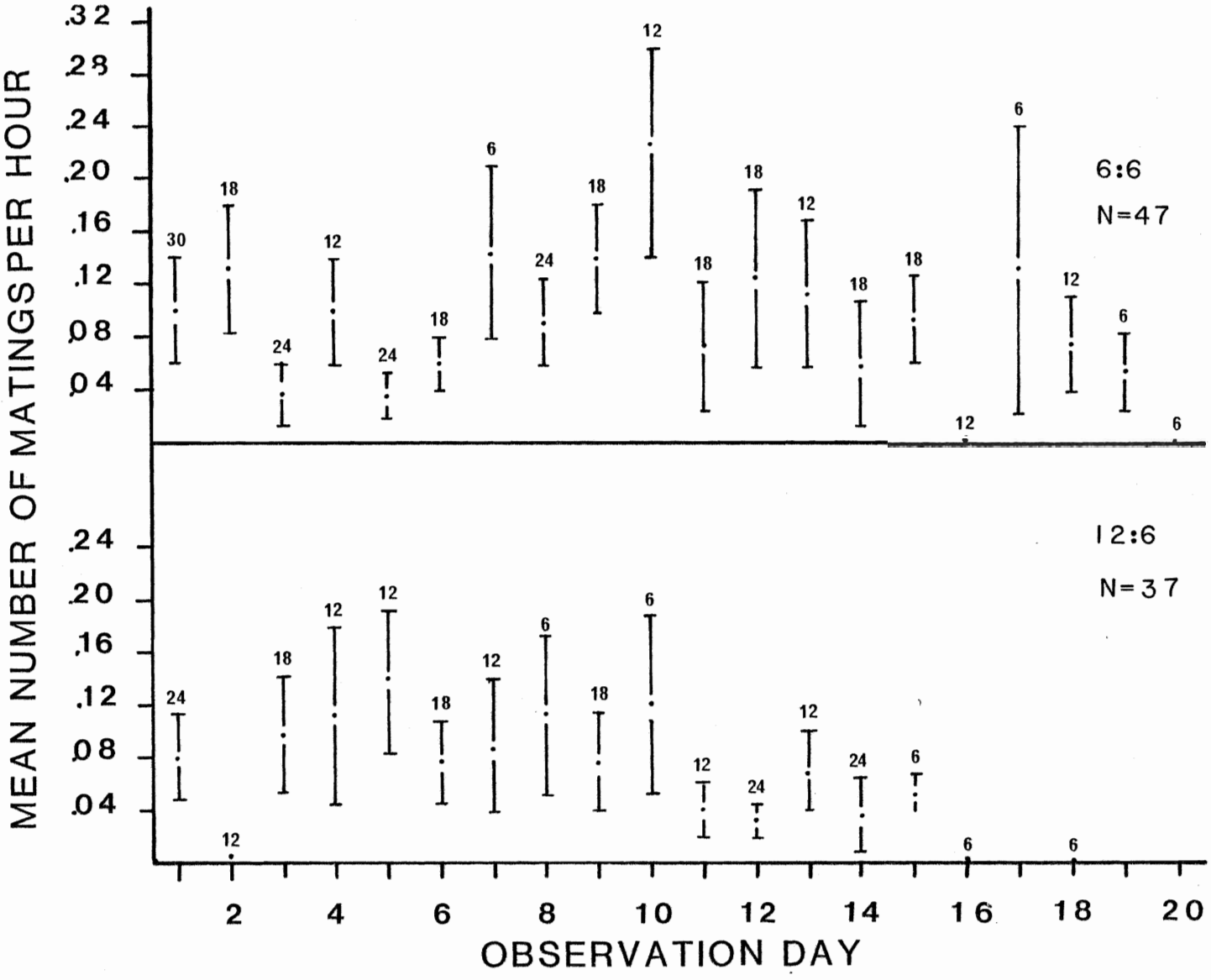
Appendix Figure 4

The mean number of matings per hour (with standard error bars) by males as a function of observation day at low (six males and six females) and high (twelve males and six females) densities. Small numbers above the standard error bars represent the number of males used to calculate the means. Fluctuations in sample size reflect variations on the day observations were conducted in replicate runs.


MEAN NUMBER OF MATINGS PER HOUR
.32
.28
.24
.20
.16
.12
.08
.04
6:6
N=45
30
18
24
12
24
12
12
24
18
12
18
12
24
18
12
6
18
6
12:6
N=70
.16
.12
.08
.04
18
24
36
24
24
36
24
12
36
12
24
36
24
48
12
24
12
2
4
6
8
10
12
14
16
18
20
OBSERVATION DAY

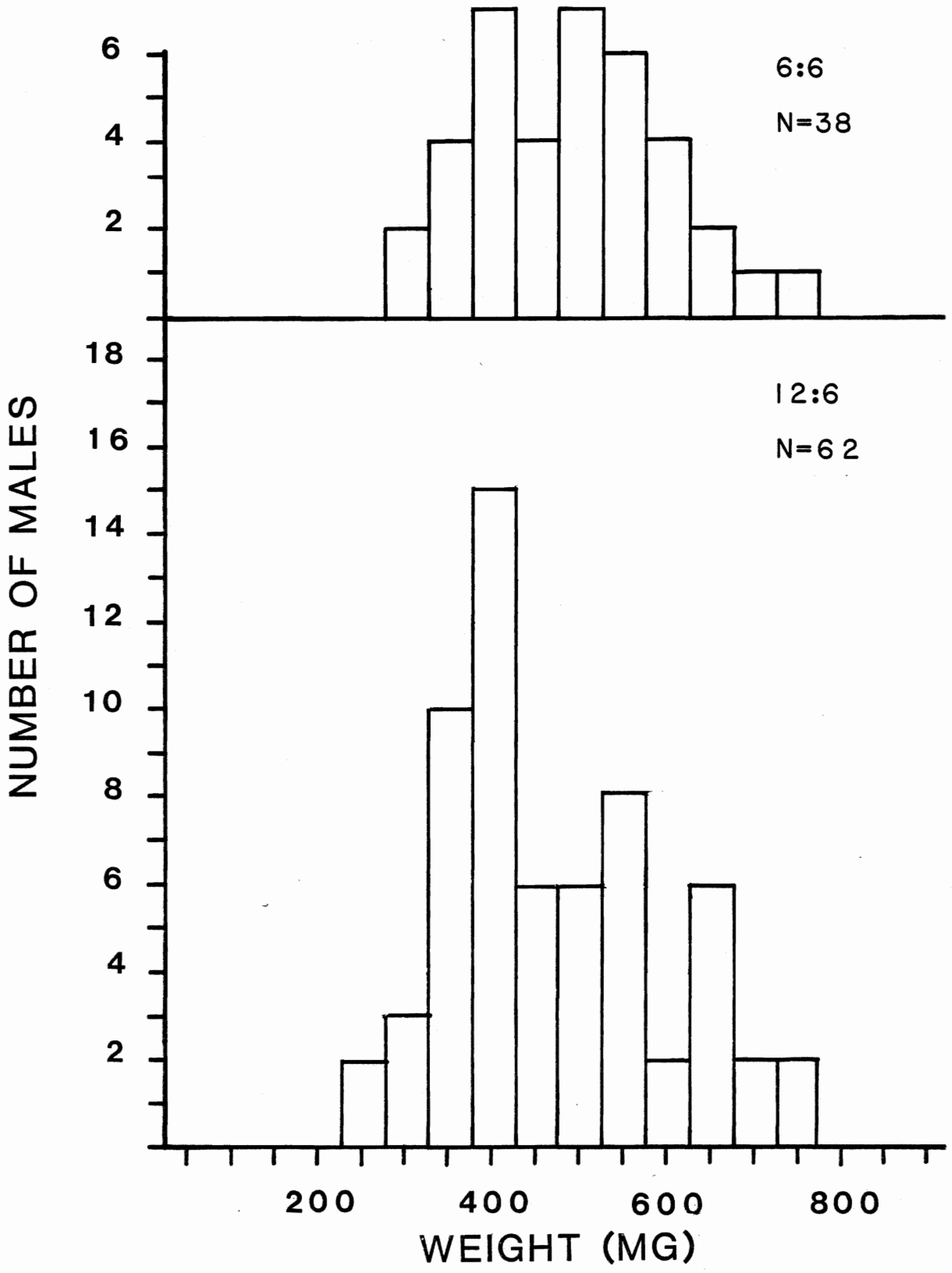
Appendix Figure 5

The mean number of matings per hour (with standard error bars) by females as a function of observation day at low (six males and six females) and high (twelve males and six females) densities. Small numbers above the standard error bars represent the number of females used to calculate the means. Fluctuations in sample size reflect variations on the day observations were conducted in replicate runs.


MEAN NUMBER OF MATINGS PER HOUR
.32
.28
.24
.20
.16
.12
.08
.04
6:6
N=47
12:6
N=37
2
4
6
8
10
12
14
16
18
20
OBSERVATION DAY

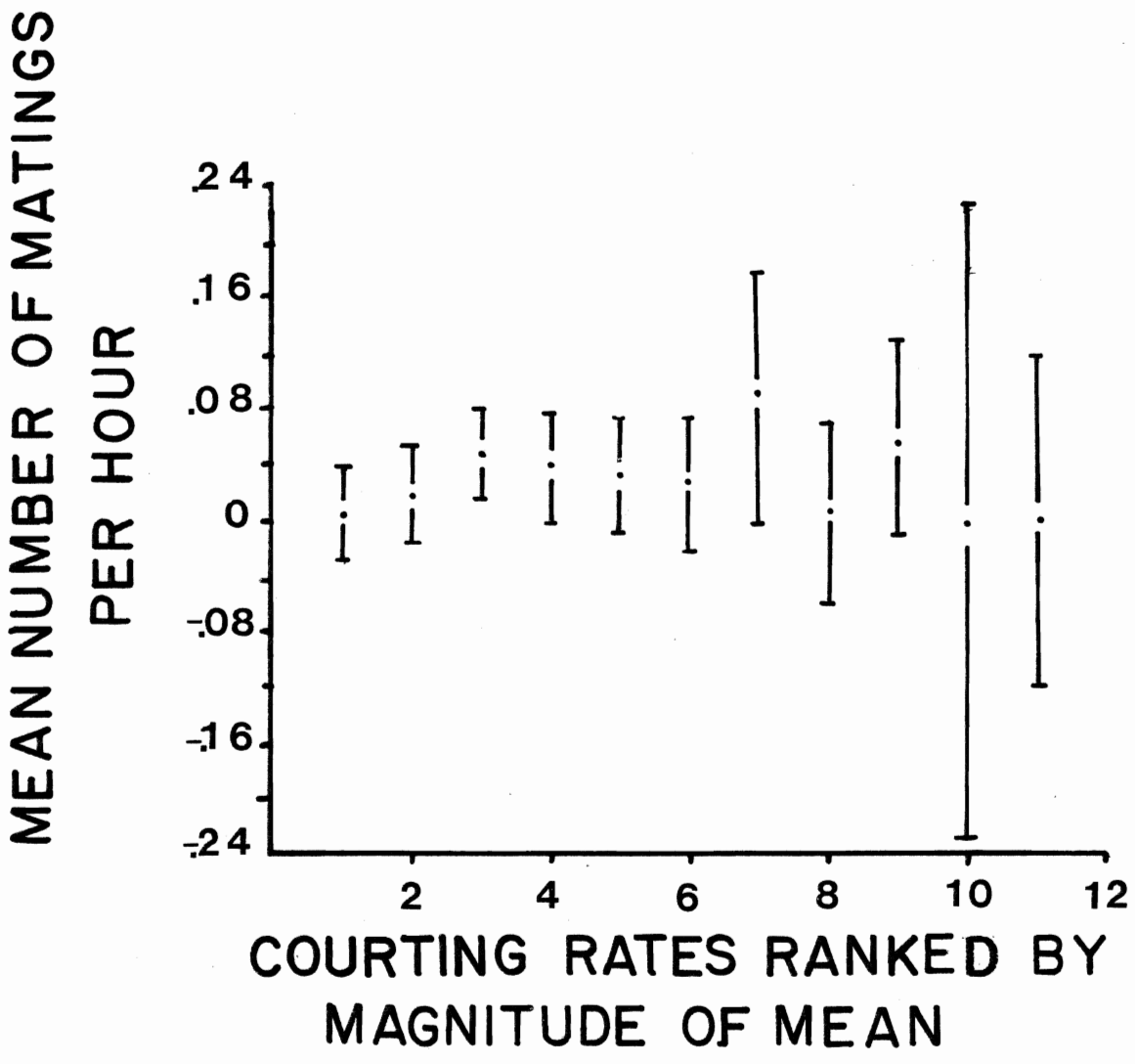
Appendix Figure 6

Frequency distribution of male weight (mg) at low (six males and six females) and high (twelve males and six females) densities.


6
4
2
6:6
N=38
18
16
14
12
10
8
6
4
2
12:6
N=62
NUMBER OF MALES
200
400
600
800
WEIGHT (MG)

Appendix Figure 7

The mean number of matings per hour by males, with upper and lower comparison limits as a function of the mean number of minutes spent courting per hour at the high density (twelve males and six females).


MEAN NUMBER OF MATINGS PER HOUR
.24
.16
.08
0
-.08
-.16
-.24
2
4
6
8
10
12
COURTING RATES RANKED BY MAGNITUDE OF MEAN